FINAL REPORT

The Potential for Restoration to Break the Grass/Fire Cycle in Dryland Ecosystems in Hawaii

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Technical Approach: Project objectives were addressed and tested in dry forest regions on the Island of Hawaii. Remote sensing methods included: (1) analysis of historical and current conditions, (2) high-resolution ecosystem mapping, (3) field validation of remotely sensed data, and (4) web-based satellite monitoring. Field-based methods addressed the potential for restoration of native species to alter ecosystem structure in a manner that will reduce fine fuels and fire danger. This field-based effort addressed the major barriers to restoration in a sequential manner across remnant native community types, and it developed and tested the effectiveness of a firebreak design that incorporates traditional fuel breaks (i.e. strips with fuels removed mechanically) grading into "greenstrips" planted with fire resistant native species.

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List of Acronyms

3D	Three Dimensional
ACORN5	Atmosphere CORrection Now
AVIRIS	Airborne Visible/Infrared Imaging Spectrometer
B	Bare Ground
C3	Photosynthesis System
C4	Photosynthesis System
CAO	Carnegie Airborne Observatory
CEMML	Center for Environmental Management of Military Lands
CIR	Color Infrared
Cleaf	Carbon Content of a Leaf
COLA	Cost of Living Allowance
DAAC	Distributed Active Archive Center

DLNR	Department of Land and Natural Resources
DoD	Department of Defense
DOFAW	Division of Forestry and Wildlife
DSM	Digital Surface Model
DTM	Digital Terrain Model
DVS	*Dodonaea Viscosa* Shrubland
ENVI	Environment for Visualizing Images
EOS	Earth Observing System
ERH	Enemy Release Hypothesis
ESRI	Environmental Systems Research Institute
ESTCP	Environmental Security Technology Certification Program
FICA	Federal Insurance Contributions Act
FLC	Fraction of Live Cover
GIS	Geographic Information System
GLM	General Linear Model
GPS	Global Positioning System
HETF	Hawaii Experimental Tropical Forest
HSI	Hyperspectral Imaging
HSM	Habitat Suitability Mode
IMU	Inertial Motion Unit
IPIF	Institute of Pacific Islands Forestry
KY	Kilo Years
LAI	Leaf Area Index
LiDAR	Light Detection and Ranging
LLC	Limited Liability Corporation
LS	Low Suitability
MODIS	Moderate Resolution Imaging Spectrometer
MPW	*Metrosideros Polymorpha* Woodland
MSDF	*Myoporum-Sophora* Dry Forest
NASA	National Aeronautic and Space Administration
NFDRS	National Fire Danger Rating System
NIR	Near Infra-Red
Nleaf	Nitrogen Content of a Leaf
NPV	Non-Photosynthetic Vegetation
Pleaf	Phosphorus Content of a Leaf
PSAG	Pleistocene Substrate Age Gradient
PSW	Pacific Southwest Station
PTA	Pohakuloa Training Area
PV	Photosynthetic Vegetation
PWW	Puu Waawaa
RAWS	Remote Automated Weather Station

RC	Resource Conservation
RCA	Radiocarbon Age
RMSE	Root Mean Square Area
SEM	Structural Equation Models
SERDP	Strategic Environmental Research and Development Program
SMA	Spectral Mixture Analysis
SON	Statement of Need
T&E	Threatened and Endangered
UAV	Unmanned Aerial Vehicle
UHH	University of Hawaii at Hilo
UHM	University of Hawaii at Manoa
USFS	United States Forest Service
wLiDAR	Waveform Light Detection and Ranging

Keywords

Greenstrips, Habitat suitability, Invasive species, Remote Sensing, Restoration planning,

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Abstract: RC-1645

Objectives: This study used remote sensing and field-based experiments to provide basic scientific information and practical tools for managing and restoring tropical dry forest landscapes on military lands in the Pacific. Results have and will continue to directly benefit the military mission in the Pacific by increasing capacity to restore native forests, thereby reducing wildfire and enhancing habitat for threatened and endangered species.

Technical Approach: Project objectives were addressed and tested in dry forest regions on the Island of Hawaii. Remote sensing methods included: (1) analysis of historical and current conditions, (2) high-resolution ecosystem mapping, (3) field validation of remotely sensed data, and (4) web-based satellite monitoring. Field-based methods addressed the potential for restoration of native species to alter ecosystem structure in a manner that will reduce fine fuels and fire danger. This field-based effort addressed the major barriers to restoration in a sequential manner across remnant native community types, and it developed and tested the effectiveness of a firebreak design that incorporates traditional fuel breaks (i.e. strips with fuels removed mechanically) grading into “greenstrips” planted with fire resistant native species.

Results: Through remote sensing the project team assessed the historical and current condition of the two major dry forest landscapes on the Island of Hawaii and provided information to assess their restoration potential. In addition to analyses of historical aerial photography, soil surveys were conducted on old Mauna Kea substrates to determine whether contemporary dominance of the native C3 shrub *Dodonaea viscosa* is a recent phenomenon that could be facilitated by a natural grass fire cycle. Radiocarbon dating of charcoal collected from these older substrates indicates that fires have occurred on this landscape for at least 7,380 years radiocarbon age (RCA) thereby predating the arrival of European and Polynesian settlers to the Hawaiian archipelago, and it demonstrates that non-anthropogenic fires occurred in Hawaiian drylands prior to human settlement and the introduction of nonnative fire-adapted grasses.

Remotely sensed products include historical maps of dry forest cover change and state-of-the-art high resolution maps of vegetation cover, topography, species dominance, and fire fuel cover for purposes of setting a clear baseline for potential restoration efforts. Using this approach, areas deemed high priority for restoration can be more intensively managed, thereby releasing low priority areas for recreation and military training. In addition, areas with high risk of fire can be targeted for appropriate fire reduction activities.

One of the most successful products was the development of a habitat suitability model (HSM) used to identify areas of the landscape where stakeholder activities can be prioritized based on biophysical and geomorphic characteristics. Using data from the Pohakuloa Training Area (PTA) staff on known locations of threatened and endangered plant species, as well as data derived from the Carnegie Airborne Observatory (CAO), habitat features (i.e. slope, leeward facing etc.) were identified that are associated with extant plant populations and suitable microclimate.

Additional uses of the remotely sensed data included the use of Global Positioning System-(GPS) collared feral goats to understand the movement ecology of these animals within these dryland systems. Although these animals follow green-up events, they also spend a disproportionate amount of their time in highly suitable sites for plants. The last remotely sensed

tool developed used a Fuel Curing Index algorithm applied to MODIS satellite data scaled between 0 and one, with high values corresponding to a historically low fraction of live cover (i.e. high fire potential). The Index provides general information about the quality and quantity of fuel in any given area throughout the year, and it can be based retrospectively on the MODIS record from 2000 to current and projecting in near real time via the web.

The experimental design of the field-based component of the project allowed an assessment of the effects of restoration on fuels in two ways. First, by comparing initial differences in fuel and microclimate conditions between plots with degraded and suitable habitat, the effects of canopy trees, and topographic position on fuels could be quantified. Second, restoration effects could be assessed by monitoring changes that occur as native cover was increased in the forest understory. This approach allowed not only determining ecosystem specific restoration prescriptions, but it also helped effectively guide resources towards breaking the grass/fire cycle. Our sites span a productivity gradient, and our results are consistent with previous work suggesting that active restoration is needed at both high and low levels of resource availability due to high competition with invasive species at high resource levels and low establishment at low resource levels.

During the experimental phase, a stand-replacing fire occurred in subalpine dry forests on Mauna Kea in Hawaii, within the PTA. A broadcast seed experiment was conducted that included species that are known to be adapted to fire and some that are not to examine their responses to restoration in these conditions. The experimental design also allowed an investigation of the role that non-native ungulates play in the restoration of this ecosystem. Overall, seed availability had the greatest impact on the recruitment of native and non-native species and the presence of herbivores had a negative effect on the recruitment of native species. Initial recruitment and plant biomass were higher in the burned site than elsewhere and may be the result of a pulse of increased nitrogen (N) that was made available following the fire; however, significant erosion of the surface soil occurred following the fire. Therefore, the plant response to the initial pulse of N may be temporary and the chronic loss of topsoil could have longer-term impacts on the development of the plant community.

A replicated field experiment was established with grass removal, shading out-planting, and seeding to determine what site preparation and planting strategies are most successful for establishing greenstrip plantings in areas dominated by grasses and devoid of tree cover. The purpose of the greenstrip study was to identify species for restoration that will reduce the incidence of invasive grasses and thus fire in dryland ecosystems. Control treatments with no plants had the highest rates of invasion, and native species addition plots significantly reduced grass re-invasion compared to the controls. Overall, greenstrips appear be a favorable technique to reduce fuel loads in degraded habitats.

Benefits: The outcomes associated with this project jointly benefit a number of land management agencies in Hawaii and the Pacific including the U.S. Department of Defense and the State of Hawaii Department of Land and Natural Resources. Specifically, direct work with the PTA environmental crew (from the Center for Environmental Management of Military Lands) supported their mission towards a commitment to preserve, protect, and enhance natural resources while improving the Army’s ability to conduct training and maintain military readiness.

1. Objectives

We combined newly developed remotely sensed information with field based studies to: 1) define the current condition and historical changes to tropical dry forest ecosystems in Hawaii, 2) develop technology for regional restoration planning and ecosystem monitoring, 3) quantify restoration potential and develop restoration prescriptions for remnant Hawaiian dry forests and shrublands, and 4) develop effective fuel and fire risk reduction measures that protect dry forest fragments and initiate succession of degraded grasslands into native woody communities. This combined synergistic approach has improved the capacity of military lands to sustain training activities by providing effective and sustainable fire risk reduction strategies.

1.1 Current condition and historical changes to tropical dry forest composition and structure in Hawaii

Our first remote sensing effort was to develop a historical map and associated publication of dry forest cover change from 1954 to present for a major dry forest landscapes on the island of Hawaii. To assess forest decline on military lands is a critical first step to developing effective management and restoration efforts. Tropical dry forests in Hawaii are threatened with extinction. The restoration of dry forest is a major focus of conservation research and management. To set dry forest restoration targets managers need to understand the historical baselines and human modifications to the landscape. We are addressed the following questions:

a. How has woody cover changed throughout dryland communities over the past 50-60 years?
b. What does this suggest about ecologically viable areas for woodland restoration?
c. What is the trajectory of vegetation composition in the *Dodonaea* shrub-land for the purposes of restoration planning in Pohakuloa Training Area, Hawaii – a regionally significant habitat for threatened and endangered dry forest species?

1.2 Developing technology for regional restoration planning and ecosystem monitoring

Our second and largest remote sensing activity was to develop a state-of-the-art high resolution map of vegetation cover, species dominance, and fire fuel cover for purposes of setting a clear baseline for potential local and regional restoration efforts. The goal with this segment of the study was to develop a set of regional restoration goals – mainly in terms of aboveground carbon storage, canopy diversity, and fire resistance – that can be used by resource managers to track the progress of the restoration experiments through time. The third remote sensing component takes advantage of high temporal frequency satellite imagery to aid in the near real-time monitoring of fire fuel conditions. We addressed the following questions:

a. What is the relationship between vegetation, topography, and fire fuel loading?
b. How do the fire fuel conditions vary with woodland community type on both a seasonal and interannual basis?

1.3 Developing restoration prescriptions that alter fuel conditions and fire risk within remnant tropical dry forests

We established a field experiment simultaneously provided baseline data on small-scale fuel conditions and potential fire behavior within a range of dry forest community types. To do this we developed strategies for establishing sustainable populations of native species, and then tested the effectiveness of restoration of native woody cover as a tool to reduce fine fuel loads and potential fire danger. To achieve these goals we applied treatments to address the major barriers to restoration (i.e. invasion of non-native grasses; lack of native species seed and/or propagules; and absence of suitable microhabitat for native species) in a replicated manner across community types. We then tested the potential for these restoration treatments to reduce fire danger. We addressed the following questions:

a. How do effective restoration prescriptions change across dryland community type and from degraded to more intact habitats?
b. Can native species restoration be used as a tool to reduce fine fuel loads, increase fuel moisture, and thereby break the fire/grass cycle in dry forests?
c. What are the seasonal movement patterns of feral goats? What plant communities do feral goats prefer, and do these preferences vary seasonally? How do feral goats respond to intra-seasonal vegetation dynamics on small temporal scales (e.g., in response to changes in plant photosynthetic activity following pulse precipitation events)?

1.4 Testing methods to reduce fire spread within highly degraded grass-dominated former dry forest

A second component of our field study was the design of effective fire reduction measures to protect remaining dry forest fragments and stop the spread of large fires across grass-dominated landscapes. Within large areas that have been completely converted to grasslands, restoration-based approaches should be targeted to enhance other fire and fuel reduction measures that are in place. Our experimental design included traditional fuel breaks (i.e. strips with fuels removed mechanically) in areas prone to ignition as well as “greenstrips” planted with fire resistant native species. To assess the potential feasibility and effectiveness of greenstripping in Hawaii, we addressed the following questions:

a. What native species are suitable candidates for use in greenstrips?
b. What site preparation and planting strategies are best to maximize success of greenstrip plantings?
c. Do greenstrip plantings reduce available fuels and alter fuel continuity in such a way as to reduce fire spread and intensity?
d. Do greenstrip plantings reduce the spread of invasive species?

2. Background

Altered fire regimes are one of the most immediate threats to remnant dry forests and shrublands in the tropics. In Hawaii for example, fires were generally infrequent and limited in size prior to human induced changes in native ecosystems (Loope 1998). Over the past century, however, wildfire frequency and size have increased dramatically as a result of invasion by fire-promoting non-native invasive grasses (Smith and Tunison 1992). These grasses increase fine fuel loads and alter fuel structure in ways that increase the likelihood of fire ignition and spread. Fire-promoting characteristics of non-native invasive grasses include: rapid biomass accumulation, high surface area/volume ratio, high dead/live biomass ratio, and ignition at high moisture levels (Fujioka and Fujii 1980, Hughes et al. 1991). Furthermore, fire effects and post-fire environmental conditions promote recruitment of these grasses and inhibit recruitment of native woody species. These changes in community structure and composition result in fuel and microclimate conditions that increase the likelihood of subsequent fire (Freifelder et al. 1998). In this way, non-native grass invasion initiates a grass/fire cycle (See Figure 1) that converts native forest to non-native invasive dominated grassland (D'Antonio and Vitousek 1992). This cycle is now considered the primary agent of forest to grassland conversion in dry and mesic plant communities in Hawaii and elsewhere in the tropics (Mack and D'Antonio 1998, Goldammer 2012, Angelo and Daehler 2013, Loope et al. 2013, Bowman et al. 2014).

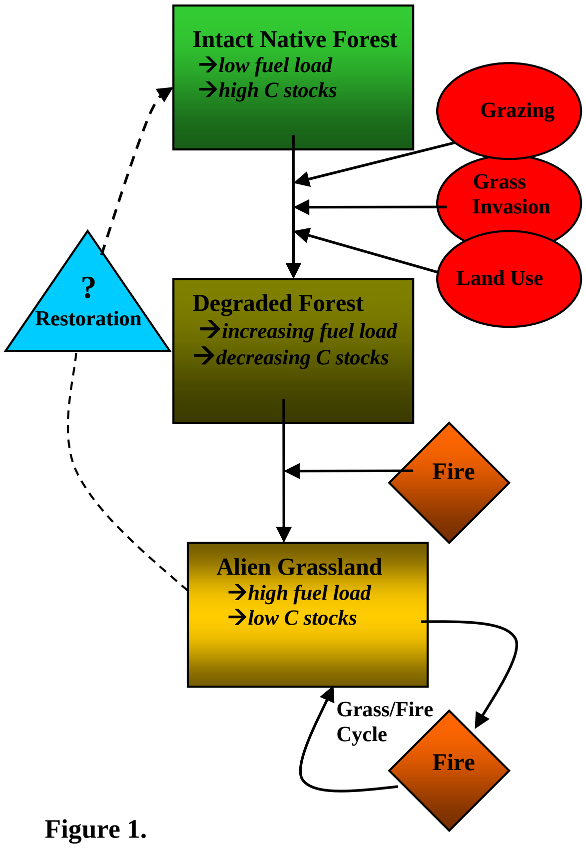


Figure 1.
Conceptual model of native forest degradation resulting in a grass/wildfire cycle maintained by fuel/microclimate feedback.

While the total area burned annually in Hawaii may be small relative to that of fire-prone areas of the US mainland, the potential damage to natural resources posed by fires in Hawaii is profound. There are more endangered species per square mile on these islands than any other place in the US, and most of these species - and the ecosystems in which they live - are found nowhere else in the world. Hawaii is home to nearly 1/3 of all federally listed threatened and endangered species and almost 1/2 of all listed plants. The total number of listed plant species in Hawaii has increased by 40% over the last six years, and over 100 of these have fewer than 20 known individuals (Loope 1998). Over 90% of the original Hawaiian dry forests have been destroyed (Mehrhoff 1993, Bruegmann 1996), and over 25% of the officially listed endangered plant taxa in the Hawaiian flora are from dry forest or dry-scrub ecosystems (A. K. Sakai and W. L. Wagner, unpublished data).

Disrupting this cycle of fire and forest loss is of utmost importance to the Department of Defense, because training induced wildfire has very large detrimental effects on military mission in tropical dry forest ecosystems. We propose that on military lands in Hawaii and throughout the Pacific, native forest rehabilitation and restoration may be the most cost-effective management tool to reduce fuel loads, fire danger, and fire impacts while also controlling invasive species establishment and spread.

Restoration of woody canopy cover is likely to reduce fire risk by altering fuel and microclimate conditions in ways that reduce the likelihood of fire ignition and spread. Since many fire-promoting non-native invasive grasses employ a C_4 photosynthetic pathway, canopy shade is likely to decrease their productivity (Knapp and Medina 1999). Our previous work in Hawaiian lowland dry forest supports this hypothesis, suggesting that increasing canopy density can reduce grass fuel biomass and flammability. Furthermore, low grass biomass produces moist microhabitat conditions that may be more suitable for less flammable species. Microclimate variables such as wind speed, generally one of the most important for predicting fire spread, can be twice as high in open grasslands as in open-canopy woodlands in Hawaii (Freifelder et al. 1998). Other studies in Hawaii and elsewhere have indicated canopy effects on temperature (Scowcroft and Jeffrey 1999) and vapor pressure deficit (Uhl and Kauffman 1990) consistent with decreased flammability.

Restoration is an attractive option for fine fuel control, because other fuel reduction methods (i.e. prescribed burning, controlled grazing, and large-scale herbicide applications) are not likely to be ecologically or economically feasible in Hawaii. While natural fires historically did occur in some Hawaiian plant communities (Mueller-Dombois 1981), most native species recover slowly, if at all, after fire and are not capable of surviving repeated fires (Smith and Tunison 1992). For these reasons, prescribed burning is likely to only temporarily reduce fuels while exacerbating problems with loss of native species and invasion of non-natives. Although intense grazing can reduce fuel loads locally (Blackmore and Vitousek 2000), grazing causes substantial damage to native vegetation (Scowcroft and Giffin 1983), contributes to loss of forest cover (Blackmore and Vitousek 2000) and has been shown to be ineffective at reducing fire frequency and severity at landscape scales. Finally, large-scale herbicide application is expensive and likely to be difficult to implement safely in landscapes containing substantial numbers of endangered native species. Thus reforestation with native species may be one of the best approaches to simultaneously accomplishing the goals of reducing fire risk from invasive grasses and reestablishing functioning native plant communities on converted sites.

3. Materials and Methods

3.0 Study Sites

Pohakuloa Training Area (PTA): Pohakuloa Training Area is located on the Big Island of Hawaii (Fig. 2) and encompasses 44,045 ha in the saddle between Mauna Loa and Mauna Kea volcanoes. It is the Army's largest and best training area in the Pacific. Most of PTA is composed of relatively young substrate from Mauna Loa. Vegetative cover varies from barren lava to dense shrub and forest ecosystems but is collectively classified as Subalpine Dryland (Bern 1995). The vegetation found in a given area is largely a function of the age of the lava flow on which it grows. Because of PTA's position largely above the inversion layer, its rainfall is considerably lower than the rain forest zone at lower elevations. The average annual precipitation across the installation is 37 cm with the highest rainfall accruing in the winter months. The annual mean temperature is about 16°C. PTA is biologically rich encompassing 24 vegetation communities. Twenty two rare plant species have been documented with 11 of those listed as federally endangered and nine as species of concern. Numerous rare and endangered fauna are also found at PTA. Critical habitat and areas of special concern in terms of their botanical composition and or habitat value for rare species have been recently designated at PTA (Stout and Associates 2002).

Puu Waawaa (PWW): The land division or ahupuaʻa of Puu Waawaa is located on the western or leeward side of the Island of Hawaii (Fig. 2) on the northern flank of Hualalai volcano. Lavas of Hualalai are primarily Holocene in age, but some deposits date to late Pleistocene (Moore and Clague 1992). The study site is at approximately 600 m elevation with a mean annual temperature around 20°C and receives approximately 60 cm annual precipitation. Botanical records for Puu Waawaa date back almost 100 years. Joseph Rock, a famous Hawaiian Botanist, conducted extensive surveys of vegetation on Puu Waawaa Ranch in 1909. At that time, he claimed that Puu Waawaa was "...the richest floral section of any in the whole Territory" (Rock 1913). Even though Puu Waawaa's forests have been greatly altered over the past 100 years, remnants of this great botanical treasure still exist. At least 182 native vascular plant species in 69 families are known from the Puu Waawaa region. Several species occur nowhere else in the Hawaiian Islands (Giffin 2003). Native plant communities in this zone are among the most diverse in Hawaii, containing many rare and endangered species. These woodlands have been greatly damaged by fire and feral animals during the past 150 years. Lama (*Diospyros sandwicensis*) is the dominant tree species. Other less common trees include alaheʻe (*Psydrax odorata*), wiliwili (*Erythrina sandwicensis*),

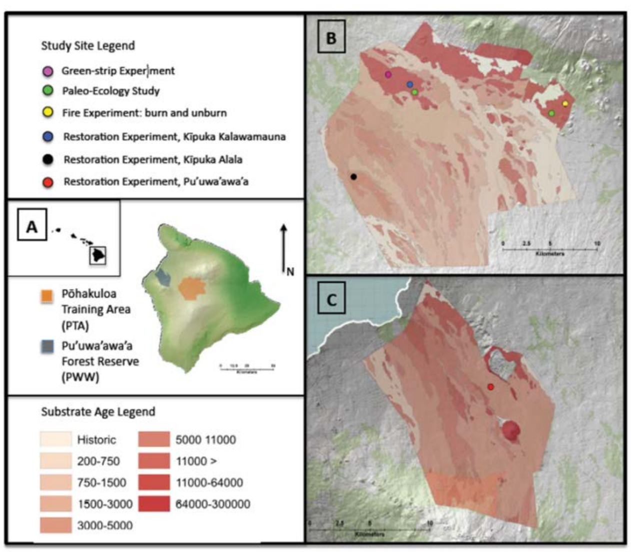


Figure 2. *Map of research sites on the Island of Hawaii (A) in Pohakuloa Military Training Area (B) and Puu Waawaa (C).*

ohe makai (*Reynoldsia sandwicensis*), and kauila (*Colubrina oppositifolia*). The rare lama and lama/kauila plant communities are restricted to this zone at Puu Waawaa.

3.1 Remote Sensing Methods

3.1.1 Historical Aerial Photography

Black and white aerial photos were acquired in October of 1954 by the United States Navy from a fixed-wing aircraft at approximately 1:52,000 and 1:42,000 scale. Original photographs were digitized at 1,000 and 1,200 dots per inch respectively. We resampled these images to 1.5 m resolution, and the study area encompassed 23 individual photographs. Due to variable solar illumination among photographs, we processed each digitized photo using Adobe Photoshop Elements version 3.1 to improve the consistency of visual interpretation and image analysis. We eliminated areas near edges with strong geometric distortion and darkening and manually adjusted image brightness and contrast to improve apparent visual consistency. We processed all images to generate a single image mosaic, which we georeferenced using ENVI 4.3 and a 2.2 m LiDAR digital terrain model (DTM, see below). Overall root mean squared error (RMSE) was 5.5 m.

Contemporary high resolution surface cover mapping

The Carnegie Airborne Observatory (CAO, Fig. 3) is an integrated airborne remote sensing and analysis system developed to acquire spatially detailed and extensive measurements of structural and biochemical properties of vegetation (Asner et al. 2007). In this analysis, it combined the airborne visible and infrared imaging spectrometer (AVIRIS) with a LiDAR sensor and 3-D navigation technology (i.e. the CAO Beta System (Asner et al. 2007). We used height measurements from LiDAR to quantify vertical and horizontal vegetation structure, and reflectance observations from the imaging spectrometer to estimate the fractional cover of photosynthetic vegetation, nonphotosynthetic vegetation, and barren volcanic substrate using methods detailed by (Asner and Heidebrecht 2002) and (Andrews et al. 2005). Airborne data were collected on January 7, 2008, which is 53 years after collection of aerial photography. The LiDAR system was configured to record the locations of up to four reflecting surfaces for every emitted laser pulse at 1.1 m laser spot spacing. Horizontal and vertical accuracy of the LiDAR system is discussed in detail in Asner et al. (2007). Laser ranges were combined with navigation information to determine the vertical and horizontal locations of reflecting surfaces. To estimate canopy height aboveground, LiDAR elevation measurements were processed to identify which laser pulses were likely to have penetrated vegetation and reached the ground surface. These points were then used to interpolate a raster digital terrain model (DTM) for the

Figure 3. *Carnegie Airborne Observatory aircraft used to collect remotely sensed data throughout PTA and PWW.*

ground surface. The remaining points were used to interpolate a digital surface model (DSM) for the vegetation canopy. Subtraction of the DTM from the DSM produced a model of canopy height aboveground (digital canopy model, DCM). The elevation models were generated at 2.2 m resolution, and all subsequent analyses were performed directly on the elevation models.

Classification of land-cover types using historical photography

We used object-based classification to distinguish four land-cover types: grasses and forbs, tall-stature woody vegetation, short-stature woody vegetation, and lava and exposed soil (Table 1). We applied a multiresolution segmentation using Definiens eCognition version 5.0. The segmentation parameters were 20, 0.8 and 0.7 for the scale factor, color and compactness respectively. We then aggregated these objects and classified image segments using a nearest-neighbor classification. Training sites were identified that described each class using field surveys and a contemporary vegetation map (Table 1).

Table 1. Land-cover classifications applied to historical aerial photography.

Grass/forb	Short-stature herbaceous vegetation cover representing grasses and forbs
Tall woody	Tall-stature woody vegetation typically exclusively *M. polymorpha*, but occasionally *S. chrysophylla* and *M. sandwicense*
Short woody	Short-stature woody vegetation dominated by *S. chrysophylla* and *M. sandwicense*
Barren	Barren volcanic substrate

Evaluation of land-cover classifications

We evaluated land-cover classifications from historical photography by comparing results to contemporary airborne remote sensing, field surveys, and vegetation maps (Shaw and Castillo 1997). We classified contemporary airborne remote sensing data into the same four land-cover classes (Table 1) by using a DCM and fractions of photosynthetic vegetation, nonphotosynthetic vegetation, and barren substrate. We also conducted field studies to determine whether classifications using historical photography and contemporary remotely sensed data accurately identified features on the ground. We visited sites in the field that were well distributed throughout the western side of the PTA landscape in November and December 2008. At each site, we traveled by four-wheel-drive and compared classification results with conditions on the ground using a hand-held tablet PC with GPS. We used features that were identifiable in the field and within imagery (such as individual trees or shrubs) to ensure that we were in the correct location in the field before determining whether classifications were accurate.

Historical change in woody vegetation

Assessment of land-cover classifications in the field using historical aerial photography indicated that they did not accurately distinguish the four land-cover classes. The only features that were consistently represented in digitized historical photos were shadows cast by large isolated objects (trees and shrubs). We therefore processed imagery from historical photos and contemporary LiDAR to generate binary classifications of tree presence and absence based on apparent shadows, and used these classifications to determine the extent and change in woody vegetation

cover. Binary images for each historical photo were created by identifying a threshold that distinguished shadows from non-shadow objects. Visual examination indicated that the threshold was 90. Therefore, we assigned all pixels ≤ 90 a value of 0 and all pixels > 90 a value of 1. Although these analyses were performed on the 1.5 m images, we aggregated pixels to summarize woody vegetation cover within units of 20 × 20 m. This aggregation was selected to produce a size that would minimize small geometric offsets between images while retaining spatial detail. We then subtracted the 2008 from 1954 aggregations to produce a map of woody vegetation change.

3.1.2 Natural and Anthropogenic Fire History

In addition to analyses of historical aerial photography, we conducted soil surveys on old Mauna Kea substrates to determine whether contemporary dominance of the native C3 shrub *Dodonaea viscosa* is a recent phenomenon that could be facilitated by a grass fire cycle. Soil samples were collected in 8 pits up to 1.5 m deep (Fig. 4) using standard methods (Chadwick et al. 2007). The study sites were selected using a high-resolution digital elevation model and airborne imaging spectroscopy from the Carnegie Airborne Observatory (CAO). Sites were identified that supported > 90% vegetation cover with descending local topography (i.e. localized areas where soil and water are likely to accumulate). These areas provide ideal sampling conditions in which we can characterize patterns in soil through time, because they represent the relatively rare places on this dryland landscape where soil accumulation occurs. We then selected 8 sites for additional sampling using a stratified random design. Because our objective was to characterize changes in the abundance of $\delta^{13}C$ isotopes as a function of soil depth, four positive control sites were those known to be dominated by contemporary C3 vegetation. Four negative control sites were dominated by contemporary C4 vegetation, which mainly consists of native and introduced grasses (e.g., *Pennisetum setaceum* and *Eragrostis atropoides*). Inclusion of positive and negative control areas allowed us to determine relationships between contemporary vegetation cover and of $\delta^{13}C$, and helps to interpret patterns as a function of soil depth.

Figure 4. *Excavating a soil pit to collect charcoal samples for isotope and radiocarbon analysis.*

In general, the soil organic matter (SOM) at the soil surface represents the isotopic signature of inputs of organic material from contemporary vegetation but is often slightly enriched due to ^{13}C fractionation during secondary metabolism and foliage senescence (i.e. lipids and lignins are generally depleted by 3-6 % relative to sugar and starch) (Ehleringer et al. 2000). Furthermore, observed changes in ^{13}C SOM values over time and with soil depth can reflect microbial incorporation (i.e. soil ^{13}C becomes more enriched (positive) over time as it is metabolized by microbes) as a progressively more significant component of the residual SOM. (Ehleringer et al. 2000). Microbial incorporation can account for up to 1.5 ‰ enrichment of $\delta^{13}C$ values. Estimating soil age accurately is further challenged by potential downward mixing of new organic matter (through biotubation, percolation, and deep deposition by roots) (Wang et al.

1996). Other likely influences include the "Suess effect" – that SOM in deeper soils originated at a time when ^{13}C values of atmospheric CO_2 were more positive and thus heavier relative to values found at the soil surface (Ehleringer et al. 2000).

Despite these assumptions, accurate interpretation of depth profiles can be greatly improved with additional data and correlations. These include; 1) analysis of % soil carbon – since grasslands, woody vegetation, and disturbance regimes such as fire differ in carbon biomass inputs in the soil – correlation of %C with ^{13}C should verify distinct patterns – i.e. Bird et al. (2000) found a significant relationship of decreased % soil C following fire (also see our data in figure 1); 2) radiocarbon dating of soil/charcoal/wood to verify age estimations; 3) phytolith identification – mixing of phytoliths into deeper soil depths is less likely than SOM due to their larger size. In addition, phytoliths of C3 and C4 species are very distinct – particularly with grasses as they are uniquely shaped (Kelly et al. 1991, McClaran and Umlauf 2000). Phytoliths form when silica or calcium precipitates in intracellular, intercellular or cell wall spaces, regularly occluding organic matter within the phytolith (Piperno 1988). The $\delta^{13}C$ values of C4 grass and C3 plant phytoliths are around -21‰ and -28‰ respectively (Kelly et al. 1991).

In Hawaii Chadwick et al. (2007) relate ^{13}C to pre and post human contact vegetation across nutrient and precipitation gradients. In the driest sites (but wetter than our PTA sites) the carbon contribution of the top 40 cm is derived from recent grass invasion – but these roots do not penetrate below 40 cm in depth (Kelly et al. 1991). Their data from SOM collected below 40cm were correlated with ^{14}C dates of 4130 and 8030 years BP and further indicate that little recent carbon has been incorporated into the SOM and that deep SOM predates Hawaiian habitation. By quantifying the relative abundance of $\delta^{13}C$ isotopes in wood, charcoal, and soil organic matter among depth profiles and between sites with different contemporary abundance of C3 and C4 vegetation, we may be able to determine whether the ratio of C3/C4 composition of the vegetation community has changed through time, infer the influence of anthropogenic versus natural factors shaping historic changes in plant communities, and radiocarbon date the approximate timing of these changes.

3.1.3 High-resolution Ecosystem Mapping

Today, digital airborne remote sensing plays a key role in Earth science, land management, and conservation because neither ground-based nor satellite measurements can fully capture the spatial heterogeneity of ecosystem structural and functional changes that occur over large geographic areas. However, the information provided by airborne remote sensing depends upon the technology and algorithms employed. In recent years, two advanced remote sensing technologies and sciences have matured to a point in which ecosystem structure and chemistry can now be quantified in ways that are useful to conservation and management. Each technology provides unique data that are sufficiently rich in information to allow for highly automated analysis techniques, including accuracy and uncertainty reporting. One technology – imaging spectroscopy (also called hyperspectral imaging) – can provide detailed information on the cover, abundance and concentration of biological materials and biochemicals (Ustin et al. 2004). The other technology – waveform light detection and ranging (wLiDAR) – can provide detailed information on the cover, height, shape, and architecture of vegetation, as well as ground topography (Lefsky et al. 2002). When combined, hyperspectral imaging and wLiDAR may

provide one of the most powerful, and ultimately practical, set of ecosystem observations available from the airborne vantage point.

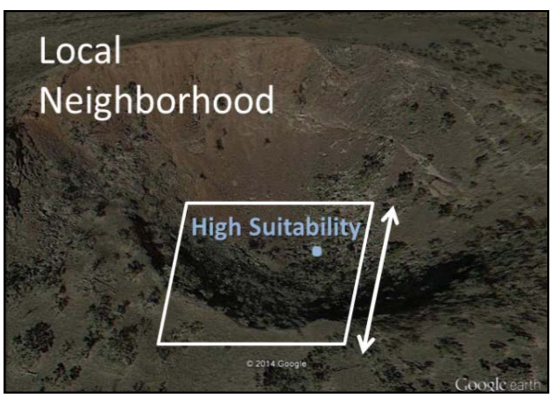
Carnegie undertook the first known effort to develop and fully integrate imaging spectroscopy and wLiDAR technologies in a new system called the Carnegie Airborne Observatory (CAO; http://cao.stanford.edu). Through in-flight fusion of these technologies on board aircraft, along with new automated algorithms for precise co-location and geo-ortho-rectification of the hyperspectral and wLiDAR data, the CAO provides an observational suite that simultaneously probes the biochemical and structural properties of ecosystems. We have tested and applied the CAO observations to Hawaiian forest ecosystems, yielding a data product suite that include underlying terrain, vegetation canopy height, 3-D canopy structure, and species dominance. Recently, Carnegie deployed the CAO to map the Puu Waawaa area in hopes of acquiring funds to analyze it at a later date. We have flown the CAO over PTA, and have analyzed the data from both PTA and PWW to deliver digital maps of topography, vegetation height, species dominance, and fire fuel load at 1.0-1.2 m spatial resolution. Topography and vegetation height are derived from the LiDAR sub-system of the CAO, whereas species dominance and fire fuel load are derived from analyses of the combined hyperspectral and LiDAR data (Asner et al. 2005). The LiDAR fires at 100 kHz, with an average laser spot size of 1.0 m from 2000 m a.g.l. An Applanix 510 inertial motion unit (IMU) and multiple GPS units are used to solve for LiDAR spot locations as projected onto the ground from the aircraft. LiDAR waveforms are geometrically corrected and subset to exclude zenith angles greater than 20 degrees from nadir. The data are then gridded at 1.0 m resolution, and a crown-finding algorithm (Knapp and Asner, unpub.) is applied to estimate the location of crown centers and edges. Canopy height is derived from LiDAR returns taken 25% inward from each crown edge, thus avoiding spurious LiDAR returns that do not penetrate to ground level. An estimated ground (bald Earth) map also will be derived using three-dimensional, terrain-sensitive algorithms and filters. The result is spatially matched top-of-canopy and ground elevation maps.

We have estimated species dominance and canopy water content from the CAO hyperspectral imagery using physically-based methods originally developed by Asner (2000), then improved and tested by Asner and Vitousek (2005), Carlson et al. (2007), and Asner et al. (2007). First, the ACORN-5 atmospheric radiative transfer model (ImSpec LLC, Palmdale, CA) was used to convert hyperspectral radiance measurements from the aircraft to apparent surface reflectance. The fractional cover of photosynthetic vegetation, non-photosynthetic vegetation, and bare substrate was then quantified in each image pixel using a fully automated spectral unmixing algorithm designed for high-fidelity imaging spectrometer observations (Asner and Heidebrecht 2002). We then ran a canopy photon transport model constrained by the fractional cover estimates (Asner and Vitousek 2005). In brief, the approach utilizes the full spectroscopic signature provided by AVIRIS to solve a 3-dimensional canopy reflectance model for canopy leaf area index (LAI), leaf spectral reflectance and transmittance properties, and leaf inclination distribution. During the radiative transfer model inversion, canopy LAI and leaf spectral properties were allowed to "float", whereas leaf inclination was fixed to an ellipsoidal distribution (Myneni et al. 1989). The model inversion adjusts the floating parameters to best match a simulated spectrum to the actual spectrum of each CAO image pixel; these best-fit parameters are then considered the best estimate of the canopy properties. A look-up table was then used to match the estimated leaf reflectance and transmittance spectra to leaf and canopy

water content (Asner and Vitousek 2005). These canopy biochemical maps were then combined with canopy structural maps from the LiDAR to estimate species dominance based on a database of species collected throughout Hawai'i (Asner et al. 2007).

3.1.4 Topographic Analysis of Endangered Species

The budget for managing endangered plant species on military land in Hawaii exceeds $10 million per year. We have the opportunity to use the high resolution data from the CAO to help guide the management and restoration of these species. Because drought stress is one of the primary limits to plant growth and reproduction in these dry ecosystems, we used elevation data from the CAO to model topographic variables associated with the evaporative stress imposed on plants by the landscape. We developed ecologically relevant criteria based on the DTM in order to define areas of suitable topography for plant restoration. Our approach differs from other approaches using species distribution modeling (e.g., MAXENT) to determine habitat suitability for specific species (e.g., Gogol-Prokurat 2011). This approach relies on existing plants that occupy patches of suitable habitat, and using the attributes of those locations to predict other suitable locations in the landscape. We do not think the assumptions of these models are realistic for our system, and for many systems with high levels of anthropogenic impacts. Species in our system likely do not occupy the areas of most suitable habitat. They occupy areas where they have escaped disturbance (training, fire, herbivory by ungulates). In addition, in dryland ecosystems many plant species benefit from similar conditions during regeneration, such as increased water availability, decreased solar radiation, and reduced evaporative stress. Therefore, we used a more general modeling approach that identifies locations in the landscape with suitable abiotic conditions that could benefit the establishment of numerous plant species. We selected two criteria for their capacity to reduce water stress. They also correspond with landscape features that restoration practitioners target to increase plant survival (K. Kawakami, pers. comm. 2010). We developed raster layers in ArcMap so that each map layer represented one criterion: 1) highly descending local topography, and 2) protection from prevailing winds (Fig. 5).



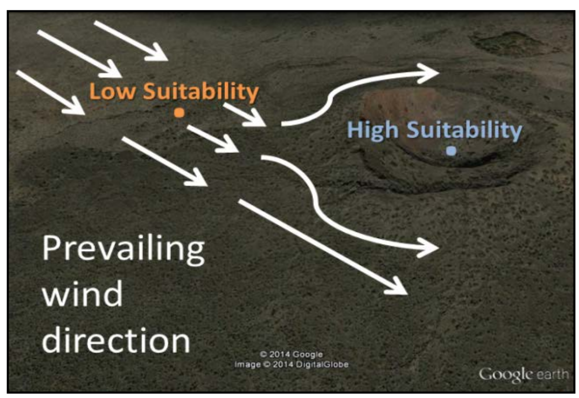


Figure 5. *The topographic variables, descending topography* **(left)** *and leeward position* **(right)**, *that were used as criteria to model habitat suitability for endangered plants. High suitability sites are located in topographic depressions and are protected from prevailing winds by topographic features.*

Highly descending local topography

We distinguished descending and ascending local topography by subtracting DTM values from the mean within a 50-m window centered on each focal pixel location. If elevation within a given

pixel is greater than the mean within a 50 x 50-m window centered on the focal location, then the focal location is characterized by ascending local topography. Similarly, if the elevation of the focal pixel is less than the mean elevation of the window it is characterized by descending local topography. If the difference between the focal pixel and the mean is 0, then the pixel is likely to represent flat ground. These analyses were performed using standard functions in ENVI 4.7. The 50 x 50-m window was selected empirically after we determined that 50 m was appropriate for the PTA landscape.

Protection from prevailing winds

We quantified exposure to prevailing winds using long-term records of monthly diurnal wind direction from RAWS weather meteorological stations. These measurements indicate that the prevailing wind direction at PTA is 67.5 degrees. Next, we calculated the degree of exposure of each pixel in the DTM to prevailing wind patterns using shaded relief modeling in ENVI 4.7. Shaded relief is typically used to simulate the appearance of natural light on a DTM from a user defined azimuth and elevation above the horizon. When applied to the azimuth of wind direction, the resultant image has pixels with low brightness in areas that are protected from prevailing winds, and high brightness in areas that are directly exposed.

Habitat suitability model

We created binary raster layers based on each criterion with a score of 1 if the condition was true and a score of 0 if false. The binary criteria layers were combined to develop a map of our habitat suitability model (HSM) for outplanting with three suitability classes: no criteria met (Class 0), one criterion met (Class 1), and two criteria met (Class 2). Field verification identified that areas with high suitability (Class 2) corresponded with leeward topographic depressions that are favored by practitioners and areas with low suitability (Class 0) corresponded with ridges and areas with high wind exposure. Thus, our digital model represented field elements important for restoration.

Model requirements

Data requirements to develop the habitat suitability model (HSM) include the following:

1. A digital terrain model (DTM) with high spatial resolution ($\leq$ 2.5 m). High spatial resolution is essential for modeling fine-scale topographic features that are important for plant growth.
2. Long-term measurements of prevailing wind direction. These data are readily available from weather stations on DoD installations.
3. Knowledge of appropriate neighborhood size for quantifying topographic variability. At PTA, we used our knowledge of the landscape based on field experience to determine the appropriate spatial scale for our analyses. Plants respond simultaneously to multiple scales, so choosing a scale for analysis requires expert knowledge that can be provided by managers of field studies at DoD installations.

Plant functional traits across suitability classes

We measured plant functional traits associated with plant growth and performance (plant height, specific leaf area, and leaf nutrients) of five common plant species in the open Dodonaea shrubland ecosystem: native shrubs *D. viscosa* and *Chenopodium oahuense*; native C4 grass *Eragrostis atropioides*; nonnative, invasive C4 grass, *Pennisetum setaceum*; and nonnative,

invasive forb, *Senecio madagascariensis*. Functional trait measurements were taken from five healthy adult individuals of each species in each of the 10 paired 8 by 45 m plots that were designated for extensive sampling from 16 June to 14 July 2011. We measured plant height by recording the distance between the base of the plant and the top of the youngest fully expanded leaf. Specific leaf area (SLA, cm^2/g) was measured using standard methods on three relatively young, but fully expanded leaves per plant (Cornelissen et al. 2003). We collected 20 relatively young, but fully expanded leaves per plant for nutrient analyses of N (Nleaf), P (Pleaf), and C (Cleaf). Samples were oven-dried for at least 48 hours at a constant temperature of 708C, ground with a Wig-L-Bug (Crescent, Elgin, Illinois, USA) and sent to UHH Analytical Lab for analysis. Nleaf and Cleaf were determined through combustion on a Costech 4010 elemental combustion system (Costech Analytical Technologies, Valencia, California, USA). Pleaf was determined by dry ashing (5008C for 5 h) of ;0.25g of sample and re-suspending in 0.5 mol/L HCl, followed by measurement of P concentrations on a Varian Vista MPX ICP OES (Agilent Technologies, Palo Alto, California, USA). We analyzed differences in functional trait measures with a general linear model (GLM) that included a random blocking term for each pair of plots, species as a random factor, suitability class as a fixed factor, and the species 3 suitability interaction term. SLA data were log-transformed to improve normality and homogeneity of variance. If the species 3 suitability class interaction term was significant, we used a Tukey posthoc test to compare differences among suitability class within each species. GLM analyses were performed in Minitab 15 (Minitab 2007).

3.1.5 Remote Sensing Tools for Restoration

The use of Earth observation systems to monitor and assess ecological value has transformed the fields of natural resource management and conservation biology (Turner et al. 2003, Corbane et al. 2015). Now, with some limitation, evaluation of changes in biodiversity, biophysical parameters and ecosystem function can be regularly examined at multiple spatial scales. Further, remote sensing has played an increasingly important role in quantifying ecosystem degradation and conservation-management outcomes towards recovery (see review by Cabello et al. (2012)). Less developed is the direct use of remote sensing technology for planning and monitoring of target-based ecological restoration and especially so in multi-functional landscapes. This may be due to the typical spatial extent of restoration ecology practice, which has historically been conceived and conducted primarily at a site-specific scale. Now with global and cross-ecosystem issues such as climate change, invasive species and pervasive land use, more landscape-scale projects are becoming the norm. Recent advances in using Light Detection and Ranging (LiDAR) to characterize objectives associated with restoration such as plant and animal habitat associations (Holbrook et al. 2015, Scott et al. 2015), hyperspectral remote sensing to identify species and plant functional performance (Asner et al. 2015, Roth et al. 2015), and the use of spatial data to assess resource variables and stakeholder interests (Brown et al. 2015, Gonzalez-Redin et al. 2016) are examples of new tools that can help to guide the field and practice of ecological restoration.

We use a case study approach in a multi-stakeholder tropical dryland restoration project to highlight the potential of remotely sensed products to quantitatively and economically guide sometimes conflicting land management priorities with stakeholder objectives. High-resolution digital elevation models derived from an airborne remote sensing platform informed land

managers tasked with endangered species restoration by guiding their efforts to highly suitable areas of the landscape where plant growth, performance and survival should be greater. Satellite-based monitoring offered a temporal approach to broadly quantify vegetation fire risk allowing a process to restrict fire promoting activities in dry landscapes most modified by fire promoting invasive grasses. Together the delineation of high suitability areas for plant based restoration, and low suitability areas for wildfire management ultimately releases moderate suitability land for alternative land uses deemed important in multi-stakeholder landscapes. To accurately assess restoration potential and aid restoration planning for a dry forest landscape in Hawaii, we integrated field experiments and surveys with LIDAR and spectroscopic measurements from the Carnegie Airborne Observatory (CAO). Specifically, we used analyses of topography and canopy density derived from the CAO data combined with current microclimate measurements to identify areas with the greatest need for restoration and areas with high potential for restoration success. Areas in need of restoration had high cover of invasive species, low cover of native species, or conditions favorable to the spread of wildfire. Areas with high potential for restoration success had conditions favorable for plant growth, such as reduced wind speeds, greater water availability, and greater shade. We developed restoration planning tools for three dryland ecosystems that reflect different restoration targets, including restoration for biodiversity, endangered plant populations, ecosystem services, and fuel prevention.

3.1.6 Web-based Satellite Monitoring

Fires in Hawai'i are fueled mainly by invasive grasses because they are perennials, and thus they maintain a large amount of aboveground live and senescent biomass throughout the year. In 2003, we developed a prototype fire fuel index at 500 m spatial resolution using 8-day NASA Terra satellite data (Elmore and Asner 2006). The Terra satellite carries the Moderate Resolution Imaging Spectrometer (MODIS), which we used with automated spectral mixture analysis (SMA; (Asner and Heidebrecht 2002)) to determine percentage cover of photosynthetic vegetation (PV), non-photosynthetic vegetation (NPV), and substrate / soil for each 500 m pixel. This was accomplished through a set of linear equations that calculates the relative contribution of each cover type to the MODIS spectral signature of each pixel. Our SMA results were shown to correspond with fuel cover from field-based and airborne measurements (Elmore and Asner 2006).

We have developed a web-based version of our previous fire fuel index algorithm that covers the entire Island of Hawaii allowing PWW and PTA land managers to both track high fire risk days for their operations, and to quantify the efficacy of woodland restoration efforts in reducing fire risk. To do this, we first improved the algorithm, and then deployed it on the web with an 8-day update provided by the MODIS data stream from NASA http://hawaiifire.stanford.edu/.

In a basic sense, fire is fueled by dead vegetation and altered by live vegetation. However, once a fire is ignited, live vegetation often forms part of the fuel bed. Because of this, a ratio of live biomass cover (PV) to total biomass cover (PV + NPV) is important. This ratio provides information both about the fire ‘damping’ effect that the live vegetation causes, as well as information about the total possible available fuel. Fraction of Live Cover (FLC) is calculated for each pixel:

$$FLC = PV / (PV + NPV)$$

There are numerous locations on the Big Island that experience grass fires; these locations are not constrained to one climatic or biological zone. These differences correspond to varying fuel bed conditions (such as different grass species). Because of this, one measure of fuel condition is not relevant across the entire island. Instead, we scaled the observed Fraction of Live Cover of each pixel to the range of historical FLC values for that one location:

$$FC = 1 - (FLC_{max} - FLC_{observed}) / (FLC_{max} - FLC_{min})$$

We believe this provides us with a Fuel Curing Index, scaled between 0 and 1, with high values corresponding to a historically low fraction of live cover (i.e. high fire potential). The Fuel Curing Index provides general information about the quality and quantity of fuel in any given area throughout the year, and can be based retrospectively on the MODIS record from 2000-2006, and projecting in near time via the web. We also have planned our algorithms to be completely automated such that the web-based fire fuel monitoring system can be maintained long after the end of the proposed project.

3.2 Field Based Methods

3.2.1 Restoration Experiment in Remnant Forests and Shrublands

We thoroughly evaluated the landscape in order to identify native dryland communities that are critical restoration targets, based on a combination of their limited geographic extent, degree of grass invasion, and strategic location for fire suppression. The following three community types were selected: *Diospyros sandwicensis* (lama)/ *Metrosideros polymorpha* (ohia) dominated forest, *Sophora chrysophylla* (mamane)/ *Myoporum sandwicense* (naio) dominated forest/woodland, and *Dodonaea viscosa* (aalii) dominated shrubland. Two of these communities can be found within the Pohakuloa Training Area and one (lama/ohia forest) is found at the Puu Waawaa site.

Within each community type, we established six blocks in fenced ungulate exclosures with similar elevation and substrates. Three of these blocks represent highly suitable habitat areas and three represent degraded habitat. We used remote sensing data and imagery analysis to locate highly suitable and degraded habitat areas. For the lama/ohia and mamane/naio ecosystems, we used LiDAR data to find highly suitable areas with dense canopy cover (upper 25th percentile of canopy cover for each ecosystem), and we located degraded blocks nearby. To our knowledge the LIDAR penetrates grasses with a leaf area index up to 3 without errors. We used field measurements of photosynthetically active radiation to quantify the effects of canopy cover on light penetration in each block. In the aalii shrubland, we used analysis of microtopography to locate highly suitable and less suitable areas based on slope, aspect, and relative topographic position. In the field, we confirmed that highly suitable topographic areas have greater soil depth than less suitable areas.

Our experimental design (Fig. 6) allows us to assess the effects of restoration on fuels in two ways. First, by comparing initial differences in fuel and microclimate conditions between plots with degraded and suitable habitat, we can quantify effects of canopy trees and topographic

position on fuels. Secondly, we can assess restoration effects by monitoring changes that occur as we increase native cover in the forest understory. This approach will allow us to not only determine ecosystem specific restoration prescriptions, but to also help effectively guide resources towards breaking the grass/fire cycle.

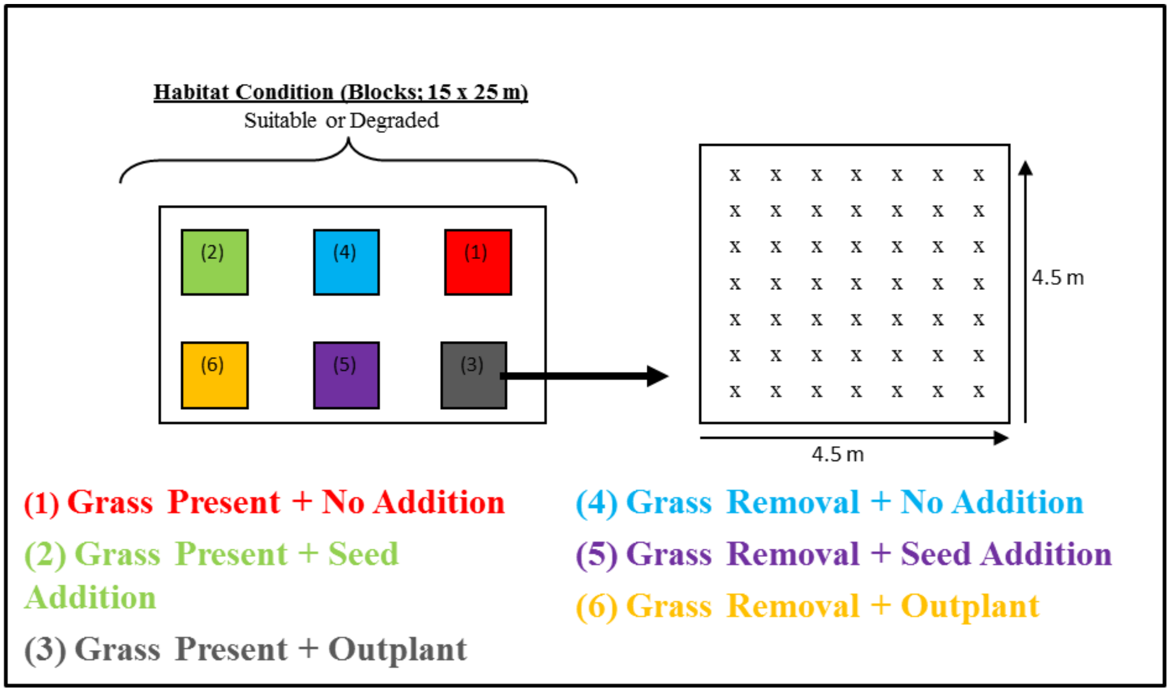


Figure 6. *Design of the restoration experiment in remnant forests and shrublands to test the effects of grass removal and native species addition within each community type and with degraded and suitable habitat (six blocks x two habitat conditions x three sites).*

The effectiveness of restoration treatments were measured as increases in native species cover, decreases in fine fuel loads and changes in microclimate. We monitored these data quarterly. Species cover estimates were collected from three 4.5-m parallel transects in each plot and are point-sampled every 50 cm. We measured surface fuelbed depth and determined fuel loads in each plot by harvesting biomass from three 0.25m by 0.25m quadrats. Biomass was dried, sorted into fuel type and size categories and weighed. We measured grass live:dead ratio quarterly for a year by clipping a 0.25m by 0.25m quadrat of grass biomass. Grass biomass was also dried, sorted into live and dead components, and weighed. Dead fuel moisture was measured by sampling litter from a 0.1m by 0.1m quadrat, using standard protocols for vegetation moisture. We installed micro-meteorological stations to record differences in wind speed, relative humidity, and air temperature between highly suitable and degraded habitats. All of these parameters will help us model the effects of restoration treatments on fire behavior, using an appropriate fire modeling system or other fire modeling procedure (Andrews et al. 2005). In addition, we measured environmental factors important for plant growth and restoration success. We measured leaf area index, photosynthetically active radiation, soil nutrients, and soil moisture in each experimental plot.

3.2.2 Ungulate Impacts

We modified our design from the original proposal by using a separate study to identify the effect of non-native ungulates on fuel characteristics and adding a movement ecology study of feral goats. This decision enhanced our project in several ways. First, there is ample evidence that ungulates negatively affect populations of native species in Hawaii, and most restoration practitioners remove ungulates at early stages in restoration. Thus, we did not find it critical to evaluate the impacts of ungulates in our experiment. Second, the removal of a fencing treatment simplified our experimental design and increased our statistical power, making the interpretation of our results more straightforward. To address the objectives of the feral goat movement ecology study the latest technology in GPS wildlife collars were used to collect accurate movement data for feral goats (Fig. 7) over a one-year period. With the use of a geographic information system, animal movement was combined with existing GIS datasets and remote sensing data from the Carnegie Air Observatory. The initial collaring process, data collection, and extensive data analysis occurred over two years, and resulted in the first comprehensive study of the movement ecology of feral goats on the Island of Hawaii. Twenty randomly selected feral goats were fitted with GPS Argos collars and monitored for one full year. Capturing and collaring the animals was completed by a professional service over a two to three day time period. Because goats are social animals with herding behavior, to maximize collar efficiency individuals from distinct herds were collared. With Argos technology, location data was transferred via satellite weekly and animals were monitored throughout the duration of the study. Animal locations were recorded every hour, allowing for a fine scale analysis of movement patterns and habitat use over the course of the study.

Figure 7. *Feral goat outside an exclosure in PTA*

As movement data was collected, a geodatabase was developed within a geographic information system (ESRI's ArcGIS software) framework. Existing environmental data was compiled, including the Carnegie Observatory's remote sensing datasets. These datasets provided a unique opportunity to determine intra-seasonal vegetation dynamics. With this geodatabase, we identified spatial variations in vegetation as well as vegetation dynamics (e.g. green-up events). Spatial and temporal variations in environmental conditions were clearly defined and correlated with animal movement data. By recording animal location data every hour, we were able to analyze movement data on several scales. Seasonal movement was monitored, along with the animal's response to smaller scale environmental changes (e.g., vegetation dynamics). We also quantified specific differences in movement types (foraging, searching, migrating, etc.). Of particular importance, this research quantifies feral goat preference for particular plant communities and included a thorough analysis of their movement. This is a novel approach in the important and growing field of movement ecology.

3.2.3 Experimental Tests of Post Burn Restoration and Invasion through Enemy Release

In August 2010, a stand-replacing fire occurred in subalpine dry forests on Mauna Kea in Hawaii, partially within the Pohakuloa Training Area. These forests are the last remaining critical habitat for the critically endangered palila honeycreeper (*Loxioides bailleui*). We used the "enemy release" experiment to also evaluate which restoration prescriptions are the most effective for restoring native plants following the burn (Fig. 8). We included species that are known to be adapted to fire and some that are not to examine their responses to restoration in these conditions. Our experimental design also allowed us to investigate the role that non-native ungulates play in the restoration of this ecosystem. DoD, Federal, and State stakeholders are actively seeking advice to manage this area, and our study will help us advise them about restoration prescriptions that will have the greatest impact on ecosystem recovery.

Figure 8. (left) *Palilia critical habitat area within PTA following the August 2010 fire and* **(right)** *the post-fire restoration study site.*

An additional objective of this experiment was to better understand what mechanism(s) controls the invasion of *Senecio madagascariensis* into subalpine dryland ecosystems of Hawaii. Non-native, invasive herbivores can create complex biotic interactions by differentially feeding on native and non-native, invasive plant species. The herbivores may act as enemies of non-native plants and prevent them from becoming invasive, or they may facilitate invasion by having a greater negative impact on native plants, compared to non-native plants. It is also possible that within the same ecosystem non-native herbivores could either facilitate or inhibit invasion under different biotic or abiotic conditions. Here, we experimentally investigate how abiotic and biotic conditions influence the effect of invasive, generalist herbivores on invasive and native plant species in a Hawaiian dry forest plant community. We used fenced exclosures to manipulate the presence or absence of invasive ungulates, and we used seed addition to manipulate the presence or absence of native propagules and the presence or absence of *Senecio madagascariensis* (*Senecio*), a non-native, invasive species. The experiment was compared between a recently burned and an unburned site in order to examine how a resource pulse following fire may alter plant-herbivore interactions (Fig. 9). Specifically, the project addressed the impacts and interactions of ungulate exclosure, propagule supply, and competitive interactions between *Senecio* and a variety of native species found in forests of subalpine dryland ecosystems including*: Sophora chrysophylla* (mamane), *Dodonaea viscosa (a'ali'i), Chenopodium oahuense*

(aweoweo), *Sida fallax* (ilima), *Eragrostis atropoides*, *Dubautia linearis*, *Plectranthus parviflorus* (‘Ala’ala wai nui), *Bidens menziesii* (koko’olau) and *Chamaesyce olowaluana* (akoko) in both burned and unburned areas. We understand that this experiment is unreplicated (i.e. on burned and unburned site) – and that the results may not be representative of all fires. However, given the opportunity to compare two sites with identical state factors we felt that the results will offer land managers an understanding of the effects of fire in this particular system of which is very prone to grass fueled fires.

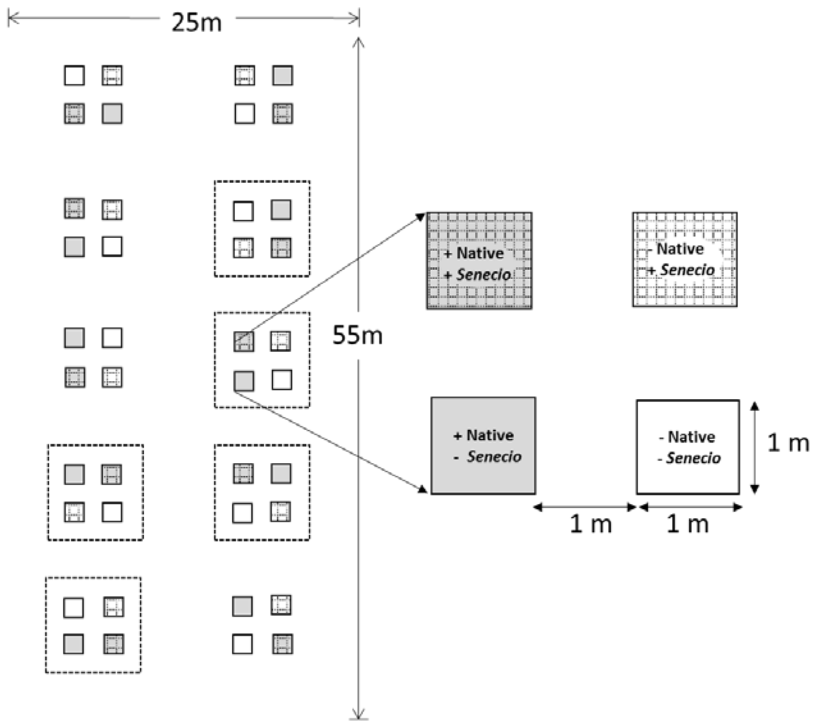


Figure 9. *Experimental design. Four 1-m² plots are grouped in each block. Dashed borders around blocks indicate ungulate-proof fencing. Plot treatments were a factorial combination of +/- Native species added as seed with +/- Senecio madagascariensis added as seed. Figure shows the design for the Burned site. The Unburned site had a similar design, although the locations of actual treatments differed due to randomization. The figure is not drawn to scale.*

3.2.4 Greenstrip Experiment

To determine what species are suitable candidates for use in greenstrips, we monitored phenology and measured fire-related characteristics of naturally occurring individuals of 6 candidate species (1 native tree: *Myoporum sandwicense*; 4 native shrubs: *Chenopodium oahuense, Dodonaea viscosa, Sida fallax,* and *Osteomeles anthyllidifolia*; and 1 native grass: *Eragrostis atropioides*). Measured traits include live fuel moisture, leaf surface area:volume ratio, canopy live:dead ratio, and heat of combustion. We are also measured traits related to species ecology, such as dispersal ability and resource competition, to understand the ecological barriers to native species restoration. We were pleased to find an adequate number of suitable candidate species. We established a replicated field experiment with grass removal, shading outplanting and seeding to determine what site preparation and planting strategies are most successful for establishing greenstrip plantings in areas dominated by grasses and devoid of tree

cover (Fig. 10). Within this experiment, we mimicked conditions (i.e. shade) that may be produced by successful greenstrip plantings to determine if these approaches will alter fuel characteristics. We also tested whether native grasses are a critical component of greenstrip plantings. Within a treeless area dominated by fountain grass, we established a grass removal area by bulldozing and spot-spraying a site next to an existing fuel break. Our experimental design included a whole-plot shade treatment with two levels (full sun or 60% shade). Within these whole plots, we had two factorially crossed split-plot treatments: one of two levels of species addition (seeding and outplanting, no addition) and one of two levels of native grass presence (seeding and outplanting, no addition). The species planted were based on preliminary results of the study of phenology and fuel characteristics and included *Chenopodium oahuense* and *Dodonaea viscosa*. Within the experimental greenstrips, we measured native plant cover, as well as changes in fuel characteristics over time. The measurements will include canopy live: dead ratio, fuel loading, packing density and continuity. These data will eventually be used within the BehavePlus or other fire modeling system (Andrews et al. 2005) to make predictions of greenstrip effects on potential fire behavior.

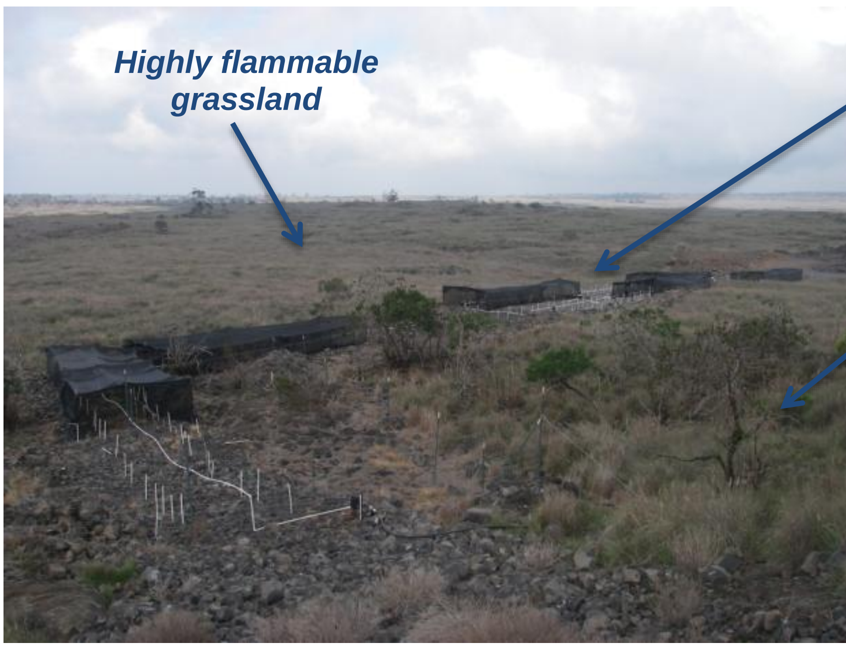


Figure 10. *The Greenstrip experiment within a highly flammable grassland environment surrounding an ecosystem fragment within PTA.*

4. Results and Discussion

4.1. Remotely Sensed Information

4.1.1. Historical Aerial Photography

We used aerial photography from 1954 and airborne LiDAR and imaging spectroscopy from 2008 to infer changes in the extent and location of tall-stature woody vegetation in 127 km^2 of subalpine dry forest on the Island of Hawaii (Pohakuloa Training Area - Fig. 11), and to identify 25.8 km^2 of intact woody vegetation for restoration and management.

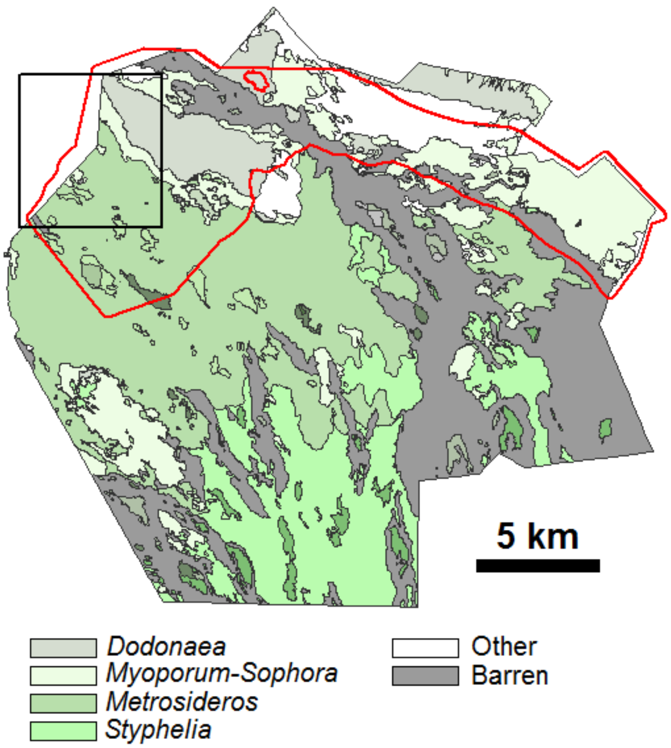


Figure 11. *Pohakuloa training area on the Island of Hawaii, showing dominant vegetation types. The extent and dynamics of woody vegetation were analyzed using contemporary airborne remote sensing and historical aerial photography in the area outlined in red (127 km^2). The area outlined in black is shown in detail in Fig. 3. The 'other' class includes Chamaesyce treeland, Chenopodium shrubland, disturbed areas, Pennisetum grassland and Eragrostis grassland.*

Field assessment of land cover classifications using historical aerial photography indicated that classification maps were not accurate (Fig. 12, Table 2). Grasses could not be distinguished from *Myoporum-Sophora* dry forest, and field studies indicated that *Myoporum-Sophora* dry forest was not consistently distinguishable from tall-stature tree communities dominated by the tree species *M. polymorpha*. We therefore focused on changes in the extent of woody vegetation (Fig. 13).

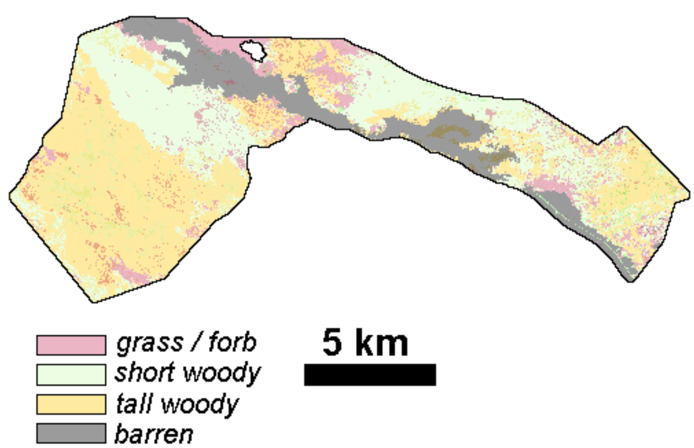


Figure 12. *Classification of historical aerial photography to distinguish grasses and forbs, tall-stature woody vegetation, short-stature woody vegetation, and barren volcanic substrate.*

Table 2. Comparison of land-cover classifications from historical aerial photography (columns) to contemporary composition (rows). Numbers are the percentage of pixels in each historical land-cover type that were represented by the contemporary community type.

	Grass/forb	Tall woody	Short woody	Barren
Dodonaea	26.6	5.7	44.1	0.9
Metrosideros	17.2	49.1	20.1	0.3
Myoporum-Sophora	46.4	43.8	32.6	18.6
Barren	9.1	1.4	3.2	80.2
Styphelia	0.6	0.0	0.1	0.0

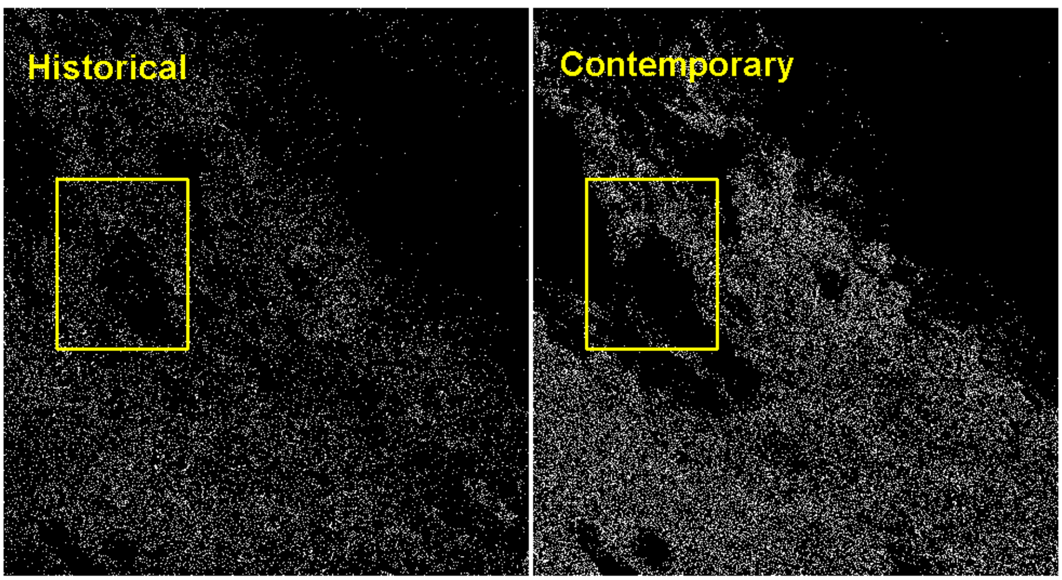


Figure 13. *Comparison of locations of tall-stature woody vegetation (individual trees) using contemporary LiDAR remote sensing (A, 2008) and historical aerial photography (B, 1954). The data are shown as binary values, where white indicates tree presence, and black indicates tree absence. The yellow box indicate areas of confirmed reduction in woody vegetation cover.*

Total cover of woody vegetation in 1954 was 54.7 km^2 and 58.6 km^2 in 2008. Approximately 28.9 km^2 underwent woody vegetation change (22.7%) between 1954 and 2008. Increases in woody vegetation cover occurred in 16.4 km^2, and 12.5 km^2 represented reduction of woody vegetation cover (12.9% and 9.8% of the 127 km^2 study area respectively). Our findings suggest that 3.9 km^2 (3.0%) experienced a net increase in woody vegetation cover between 1954 and 2008.

Although some areas of the landscape may have experienced regrowth of woody vegetation during the 53 year interval, visual assessments and field studies suggested that LiDAR data were capable of detecting trees and shrubs that were obscured within historical aerial photos, so that some apparent regrowth could be attributable to improved detection of small trees and shrubs using LiDAR. In addition, the crown area of trees detected by LiDAR was larger than the area of

the same trees estimated using historical imagery (data not shown). Analysis of reductions in vegetation cover is conservative with respect to these sources of uncertainty.

Some areas now dominated by shrubs formerly contained taller, arboreal canopies. This is apparent for a 36 km^2 sample based on a visual examination of Figure 14, which indicates spatial correspondence between areas of net reduction in woody vegetation cover and communities represented by the tree species *M. sandwicense*, *S. chrysophylla*, and *M. polymorpha*. Few changes were detected in shrubland communities currently dominated by *Dodonaea viscosa*.

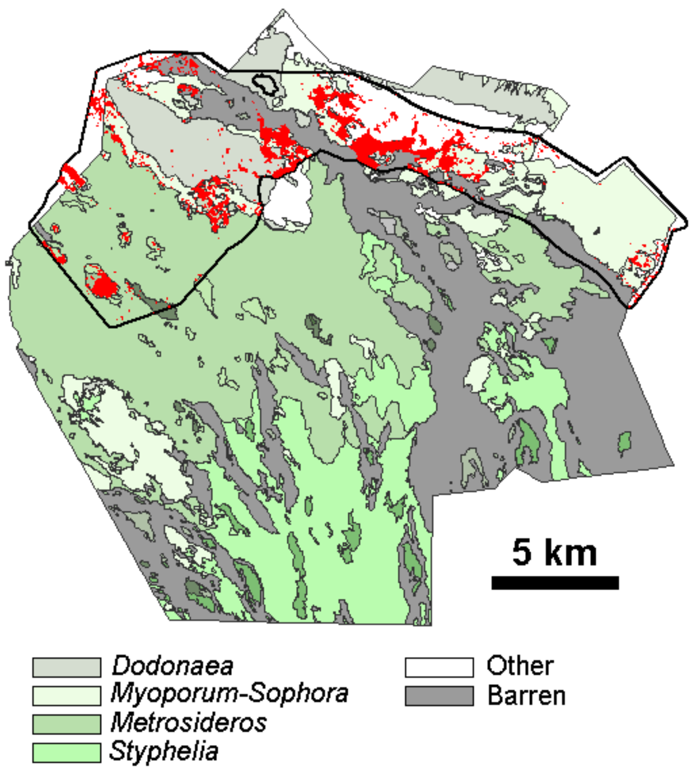


Figure 14. *Net reduction in woody vegetation cover between 1954 and 2008 (red areas). Many apparent changes were associated with short-stature woody vegetation and could be spurious. Field studies indicate that spurious changes were restricted to short-stature woody vegetation dominated by the tree species S. chrysophylla and M. sandwicense.*

Spatial patterns suggest that fires may be the primary driver of reductions in woody vegetation cover. Increases could be due to regeneration of dry forest trees or measurement errors associated with historical imagery. Areas remaining in woody vegetation cover over the 53-year study interval can be targeted for restoration and management. Although our original objective was to quantify vegetation changes in both woody and non-woody communities during a period of increased fire frequency and size in Hawaii (Larosa et al. 2008), a number of challenges restricted our analysis to tall-stature woody vegetation. Below, we discuss the nature of these limitations, and suggest additional studies that would help to improve the estimates reported here, or eliminate sources of uncertainty.

Problems directly related to historical aerial imagery were the most serious limitations. First, the historical photos are a crude brightness metric. This means that dark objects appear to be black in the images, and light objects appear to be white. Intermediately illuminated objects take on

shades of grey. This is inherently limiting, because the relationship between brightness and vegetation cover is complex. Woody vegetation, such as individual tree canopies, appeared as dark objects within historical photos. However, photosynthetic grasses were bright and closely matched with barren soil, so that simple thresholds could not be used to distinguish vegetated from non-vegetated parts of the image. In addition, the 1954 aerial photography was acquired when the sun angle and camera orientation caused inconsistent illumination within photos. This presented challenges to a comprehensive and internally consistent analysis. Analyses of spatial variability could be used in cases where there are complex associations between vegetation and brightness, but highly variable lava substrates at PTA confounded this approach as the lava range in color from light red to deep black (depending on substrate age and oxidation of iron) and vary in shape from smooth pahoehoe to rough a'a boulders.

Using shadows as a proxy for woody vegetation cover improved classification accuracy within tall-stature *M. polymorpha* woodlands, but the approach was prone to uncertainty in other woody communities. Crowns within *Myoporum-Sophora* dry forests are typically < 5 m in height, and appeared to cast larger shadows than *M. polymorpha*. Because differences in shadow sizes were restricted to historical imagery, this created potential for overestimation of the frequency of woody vegetation loss in *Myoporum-Sophora* dry forests relative to *M. polymorpha* woodlands. In addition, substrates associated with *M. sandwicense* and *S. chrysophylla*, which are older substrates with substantial soil development in comparison to *M. polymorpha* woodlands (Stemmermann and Ihsle 1993) were sometimes difficult to distinguish from vegetation. Contemporary classifications based on fractions of photosynthetic vegetation and non-photosynthetic vegetation also produced poor accuracy. Field checks confirmed that there was substantial overlap between classes, primarily because grasslands were photosynthetic at the time of image acquisition, so that signals associated with grasses and woody vegetation were not consistently expressed in fractions of photosynthetic and non-photosynthetic vegetation. Because dry landscapes in Hawaii have strong seasonal patterns in vegetation phenology (Elmore and Asner 2006, Kellner et al. 2011), future efforts should attempt to minimize differences in phenology between dates of image acquisition if the objective is a direct comparison of vegetation structure or cover.

Finally, the short-stature of shrublands at PTA created challenges for LiDAR estimation of vegetation height in these areas. The configuration of the LiDAR system at the time of data acquisition prevented detection of inbound pulses < 2 m apart. Because large areas of the landscape at PTA contain shrub vegetation that is < 2 m in height, this effectively meant that it was impossible for the sensor to receive a ground return and vegetation return for a single laser pulse in these areas of the landscape. Combined with the fact that shrub canopies lack complex heterogeneity of taller forests or isolated trees, it is possible that laser returns from shrub canopies could have been misclassified during data processing as ground returns, leading to an underestimation of vegetation cover based on LiDAR data. Therefore, the use of LiDAR data was the most effective for woody classification in tall-stature *M. polymorpha* communities, similar to the use of aerial photography.

The results of this study have shown how historical and contemporary remotely sensed data can be integrated to characterize changes in the extent of tall-stature woody vegetation in a tropical dry forest landscape. These findings suggest a 3.9 km^2 (3.0 percent) net increase in the extent of

tall-stature woody vegetation. More importantly, they indicate that 25.8 km^2 of the landscape remain in woody vegetation cover. These areas can be targets for conservation or restoration activity. Further studies should assess in detail the nature of LiDAR sampling within short-stature woody communities and should target image acquisition during intervals when phenology patterns will be distinct among classes of interest.

4.1.2. Natural and Anthropogenic fire history

Radiocarbon dating of charcoal collected from 65 ky shrubland indicates that fires have occurred on this landscape for at least 7,380 years RCA (Fig 15). This unambiguously predates the arrival of European and Polynesian settlers to the Hawaiian archipelago (Burney and Burney 2003), and demonstrates that non-anthropogenic fires occurred in Hawaiian drylands prior to human settlement and the introduction of nonnative fire-adapted grasses.

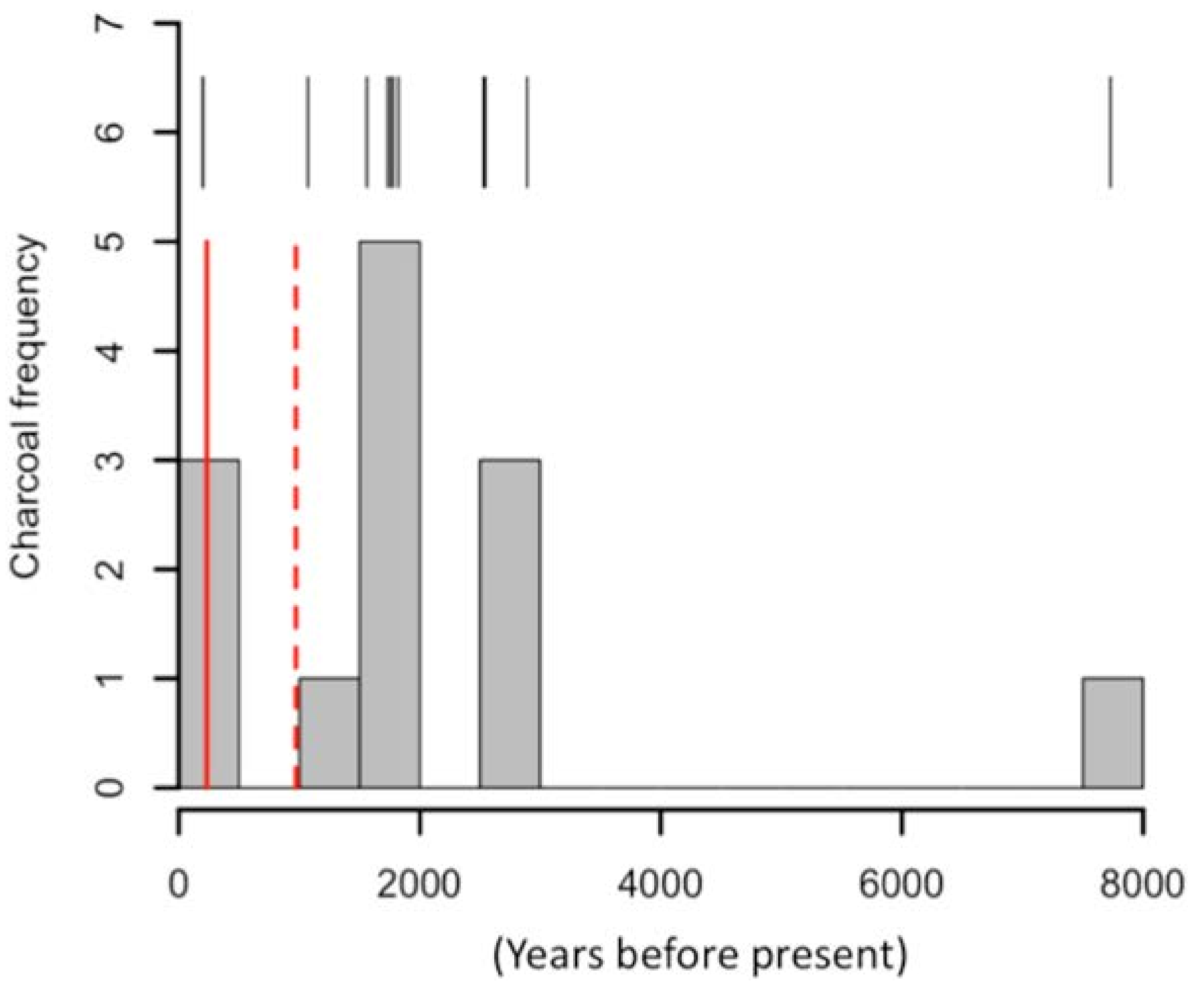


Figure 15. *14C age frequency distribution for 18 macroscopic charcoal fragments excavated from Pleistocene-aged soils. Black vertical lines indicate charcoal ages. Red vertical lines indicate the timing of arrival of Europeans (solid) and Polynesians (dashed) to the Hawaiian archipelago.*

Limited evidence suggests that some native species in Hawaii exhibit characteristics that may be adaptations to fire. For example, the two most common native species on Pleistocene-aged

substrates in our study were the native C4 grass *E. atropoides*, which accounted for 23.3% of fractional vegetation cover, and the shrub *D.viscosa*, which was 12.8% (Kellner et al. 2011). The shrub *D. viscosa* is fire tolerant (Ainsworth and Boone Kauffman 2009), and quantities of standing dead biomass and leaf moisture in *E. atropoides* are similar to the invasive fire adapted grass *Cenchrus setaceus* (E. Questad, unpublished data). We found little evidence of surface charcoal in *Metrosideros polymorpha* woodland (MPW) on historic substrates, but surface charcoal was abundant in *Myoporum-Sophora* dry forest (MSDF) and *Dodonaea viscosa* shrubland (DVS) on Pleistocene-aged soils. This observation was also made by Stemmerman and Ihle (1993) and may indirectly indicate the variation in fire frequency and risk on this substrate age gradient.

The dominance and eventual replacement of *M. polymorpha* on young substrates is relatively well understood. *M. polymorpha* is believed to be a poor competitor for water under dry conditions and may be poorly adapted to recovery after fire (Stemmermann and Ihsle 1993). The relatively barren conditions on young substrates where *M. polymorpha* dominates preempt the establishment and spread of fires, but substrates of intermediate age that support extensive dry vegetation may carry fires that remove *M. polymorpha* colonists (Stemmermann and Ihsle 1993). On older substrates, our understanding of processes responsible for the transition from dry forests dominated by *M. sandwicense* and *S. chrysophylla* (MSDF) to short-stature communities dominated by *D. viscosa* and native grasses (DVS) is more limited. Data from airborne imaging spectroscopy indicate that locations with substantial coverage of dry plant material are more densely packed on older substrates (Table 3). Furthermore, this landscape is directly in the flow path of Mauna Loa, which is one of the most active volcanoes on earth. Mauna Loa has erupted 39 times since 1832 (Rhodes and Lockwood 1995). Flows < 0.30 ky intersect Pleistocene-aged substrates on the PSAG at least five times, and intersect substrates of 3–5 ky at least three times. Thus, older substrates contain both the ignition sources and fuel conditions to facilitate grass-fueled fires, despite the fact that they are dominated by species that are native to the Hawaiian Islands.

Table 3. Mean distance (m) 2,000 randomly selected locations on substrates of the Pohakuloa substrate age gradient and the nearest location with at least 25%, 50% or 75% lateral cover of NPV.

		Mean distance (m)		
Substrate age	**Substrate type**	**25% NPV**	**50% NPV**	**75% NPV**
< 0.30	A'a	124.7 (81.6)	158.8 (82.4)	350.7 (163.2)
	Pāhoehoe	249.5 (145.3)	369.6 (154.4)	603.0 (298.4)
0.75–1.5	A'a	15.8 (13)	191.8 (135.3)	473.2 (180.1)
	Pāhoehoe	4.7 (4.6)	44.5 (41.0)	262.9 (170.6)
1.5–3	A'a	5.9 (5.1)	36.8 (31)	189.4 (159.7)
	Pāhoehoe	3.5 (3.6)	23.1 (28.1)	176.9 (148.7)
3–5	A'a	9.9 (6.9)	50.9 (20.7)	(105.7 (33.0)
	Pāhoehoe	12.0 (13.3)	48.4 (36.2)	214.3 (126.8)
Pleistocene	Older volcanic rock	3.5 (4.0)	16.1 (24.1)	108.0 (151.5)

Standard deviation provided in parentheses. Because NPV in this landscape is mainly fine fuels, these numbers demonstrate that a gradient in susceptibility to fire is associated with substrate age.

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Our data also indicate that the rate of ecosystem development is dependent on substrate topography. Substrate topography was identified by Jenny (1941) as one of five state factors that dictate soil formation. Previous studies have suggested that micro topography can influence rates of primary succession and ecosystem development (Aplet and Vitousek 1994). We found that pāhoehoe substrates accumulated both lateral cover and vertical stature of vegetation more rapidly than a‘a lava types. This interpretation is based on comparing the percentage cover and height of vegetation on pāhoehoe and a‘a substrates of the same age and lava type (Fig. 16, Table 4). Pāhoehoe substrates contain relatively smooth, undulating micro-topography in comparison to the rough, broken surface of a‘a. We suspect that one reason why primary succession might proceed more quickly on pāhoehoe substrates is that undulating texture of pāhoehoe allows water to pool, and directs water flow into cracks where plant growth is possible. Taken together, evidence of prehistoric fires in this landscape indicates one mechanism by which the vertical stature of vegetation on old, dry substrates could be reduced. It is well known that fires can also cause nutrients to become volatilized when heated, whereas others may be transported off-site in ash. To what degree fires may be influencing the ecosystem structure and productivity in this landscape through nutrient losses is beyond the scope of this paper. However, the data presented here demonstrate that the pattern of primary succession on a dryland substrate age gradient in Hawaii could be responding to a long history of fire.

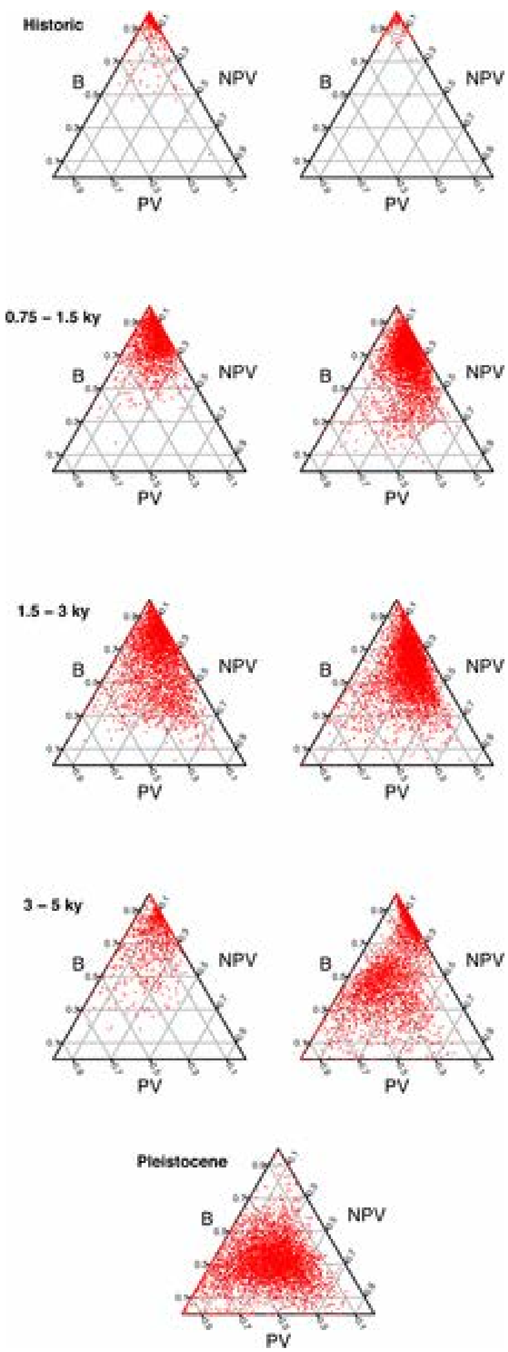

Figure 16. *Relationships among types of lateral vegetation cover. PV = photosynthetic vegetation; NPV = non-photosynthetic vegetation; B = barren substrate. The youngest substrates are dominated almost exclusively by B, but accumulate NPV and PV during primary succession and ecosystem development. The rate of development is faster on pāhoehoe (right column) than on a‘a (left column). Pāhoehoe and a‘a lava types are not distinguishable on the 65 ky Pleistocene aged substrates.*

Table 4. Distributions of lateral vegetation cover on substrates of the Pohakuloa substrate age gradient.

			Percentage of lateral cover									
Substrate age	Substrate type	Vegetation type	0–10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
< 0.30	A'a	PV	99.0	0.6	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0
		NPV	94.7	4.8	0.3	0.1	0.1	0.0	0.0	0.0	0.0	0.0
0.75–1.5	A'a	PV	84.7	10.6	3.3	0.9	0.3	0.1	0.1	0.0	0.0	0.0
		NPV	35.5	52.6	10.6	1.1	0.2	0.0	0.0	0.0	0.0	0.0
1.5–3	A'a	PV	63.7	18.9	10.1	4.6	1.7	0.6	0.2	0.1	0.0	0.0
		NPV	19.3	44.3	19.4	9.2	5.3	2.0	0.5	0.1	0.0	0.0
3–5	A'a	PV	83.1	7.3	4.6	2.5	1.3	0.6	0.4	0.1	0.0	0.1
		NPV	31.3	57.0	8.4	2.5	0.6	0.1	0.0	0.0	0.0	0.0
< 0.30	Pāhoehoe	PV	99.5	0.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		NPV	98.1	1.8	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.75–1.5	Pāhoehoe	PV	61.3	25.9	8.2	2.7	1.1	0.5	0.2	0.1	0.0	0.0
		NPV	10.6	43.1	28.6	11.6	4.9	1.0	0.1	0.0	0.0	0.0
1.5–3	Pāhoehoe	PV	42.3	36.5	12.3	4.3	2.2	1.2	0.6	0.3	0.2	0.1
		NPV	7.7	25.2	32.2	22.0	9.3	2.8	0.7	0.1	0.0	0.0
3–5	Pāhoehoe	PV	56.5	5.8	10.5	11.0	7.8	4.2	2.1	1.1	0.5	0.4
		NPV	23.6	49.7	15.8	6.3	3.0	1.2	0.3	0.1	0.0	0.0
Pleistocene	Older volcanic	PV	1.3	6.8	21.8	26.6	18.4	10.1	5.7	3.7	2.5	3.2
	rock	NPV	16.1	14.6	22.4	23.8	14.4	6.1	2.0	0.5	0.1	0.0

doi:10.1371/journal.pone.0123995.t003

4.1.3. High-resolution Ecosystem Mapping

Spectroscopic measurements were collected by the CAO in January, 2008. Hyperspectral radiance was converted to apparent surface reflectance using the ACORN-5 radiative transfer model (ImSpec LLC, Palmdale, CA). The fractional cover of photosynthetic vegetation (PV), nonphotosynthetic vegetation (NPV) and bare substrate (B) were then quantified in each image pixel using a fully automated spectral unmixing algorithm. The resultant image provides spatially detailed information on the extent and condition of vegetation cover throughout the entire PTA landscape. In 2010 we transferred user friendly data products to the Hawaii based DoD. These products show contemporary vegetation cover, species dominance, fire fuel load at 2.2 m spatial resolution, and accurate topographical information derived from remote sensing efforts which will allow land managers to quantify factors such as slope, and aspect with species distributions. A 1 km^2 sample of the PTA landscape is shown in Figures 17 and 18.

A manuscript based on this product and satellite monitoring is published in Ecological Applications. The manuscript incorporates a large-scale experiment to quantify impacts of ungulate removal on plant growth and performance, and tests whether elimination of non-native feral goats facilitated the success of invasive species. Escape from natural enemies is a leading hypothesis (Enemy Release Hypothesis, ERH) to explain the success of non-native invasive plants. Because both specialist and generalist enemies should have differential impacts on the success of native and non-native plants, and the hypothesis assumes that specialist enemies of non-natives will be rare in the introduced range, the hypothesis predicts that generalist enemies will have a greater impact on native than non-native species (Keane and Crawley 2002). This prediction follows from the assumption that native species are regulated by specialist and generalist enemies, but that non-natives are regulated mainly by generalists.

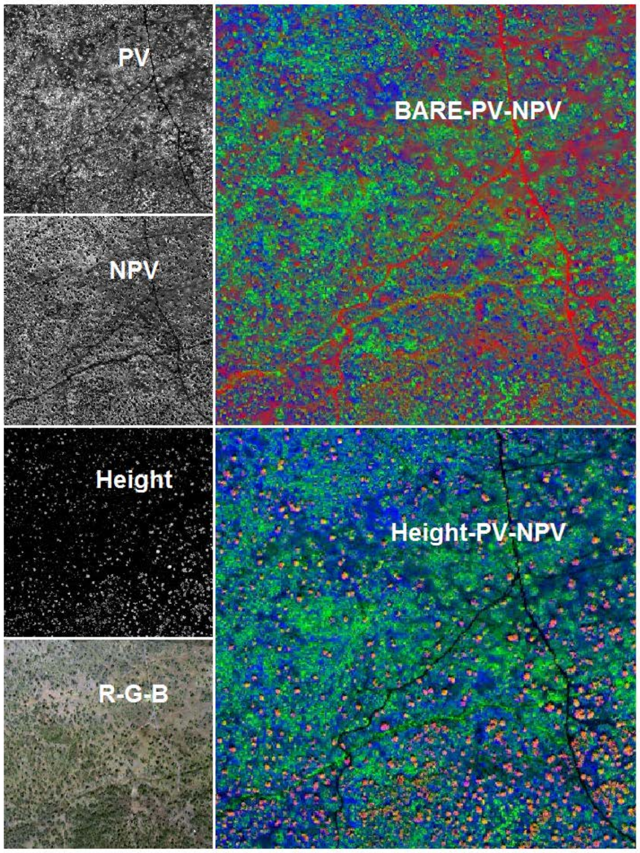

Figure 17. *Data from new remote sensing technology and the Carnegie Airborne Observatory can be used to map the location and abundance of fire fuels in a tropical dry forest landscape at high spatial resolution. All images are the same 1 km^2 sample of tropical dry forest at PTA. Images on the left show fractional estimates of photosynthetic vegetation (PV) and nonphotosynthetic vegetation (NPV), followed by canopy height from LiDAR and a natural color composite image. PV and NPV were estimated using a fully automated spectral unmixing algorithm applied to CAO data. Images on the right are color composites, which allow visualization of three components in a single image. In the top image, red is barren substrate, green is PV and blue is NPV. In the bottom image, red is height from LiDAR, green is PV and blue is NPV. Lines dissecting the image are military training road.*

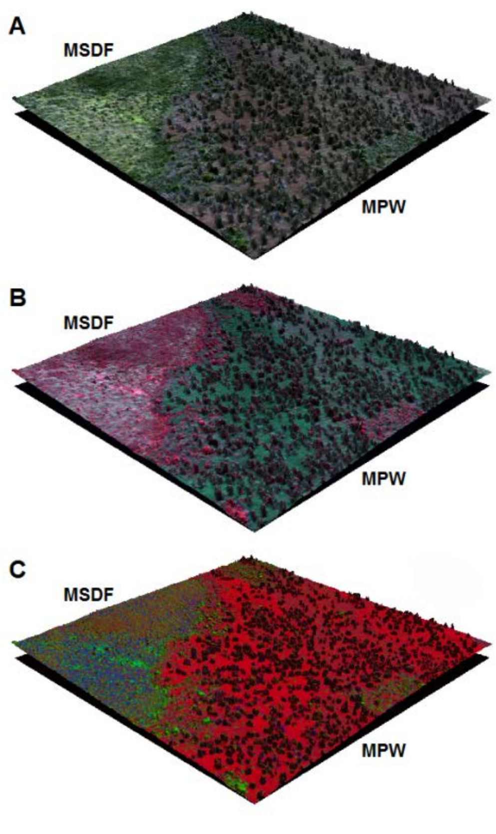

Figure 18. *Imaging spectroscopy and LiDAR show the vertical distribution of vegetation in a tropical dryland ecosystem. Each image is a 1 km^2 sample of tropical dry forest in Hawaii mapped at 2.2 m resolution. Data show samples of a managed area dominated by M. sandwicense and S. chrysophylla dry forest (MSDF) and adjacent M. polymorpha woodland (MPW). The top image (A) is a natural color composite resembling a traditional aerial photograph. The middle image (B) is color-infrared, and shows regions of high vegetation cover using NIR reflectance (pale reds and pinks). The bottom image (C) was processed to quantify PV (green), NPV (blue) and barren substrate (red). Effects of substrate age and biological invasion are clearly distinguishable between MSDF and MPW.*

We used a large-scale field experiment to test whether release from generalist herbivores (non-native feral ungulates) facilitated the success of non-native invasives in a subalpine tropical dryland ecosystem in Hawaii. Assessment of impacted and control sites before and after ungulate exclusion using airborne imaging spectroscopy and LiDAR, time series satellite observations, and ground-based field studies over nine years indicated that removal of generalist herbivores facilitated non-native success, but the abundance of native species was unchanged.

Answering this question is important, because non-native species contribute substantially to fire fuel cover in PTA. Our assessment of impacted and control sites before and after ungulate exclusion using airborne imaging spectroscopy and LiDAR from the Carnegie Airborne Observatory, time series satellite observations and ground-based field studies over nine years indicated that removal of feral goats facilitated increases in non-natives, but the abundance of native species was unchanged. Vegetation cover < 1 m in height increased in ungulate-free areas from 48.7 ± 1.5% to 74.3 ± 1.8% over 8.4 years, corresponding to an annualized growth rate of $\lambda = 1.05 \pm 0.01 \cdot \text{year}^{-1}$. Native plants experienced no significant change in cover (23.0 ± 1.3% to 24.2 ± 1.8%, $\lambda = 1.01 \pm 0.01 \cdot \text{year}^{-1}$). Time series of satellite phenology were indistinguishable between the treatment and a 3.0 km^2 control site for four years prior to ungulate removal, but diverged immediately following exclusion of ungulates (Fig. 19). Field studies and airborne analyses showed that the dominant invader was *Senecio madagascariensis*, an invasive annual forb that increased from < 0.01 to 14.7 % fractional cover in ungulate-free areas ($\lambda = 1.89 \pm 0.34 \cdot \text{year}^{-1}$), but which was nearly absent from the control site.

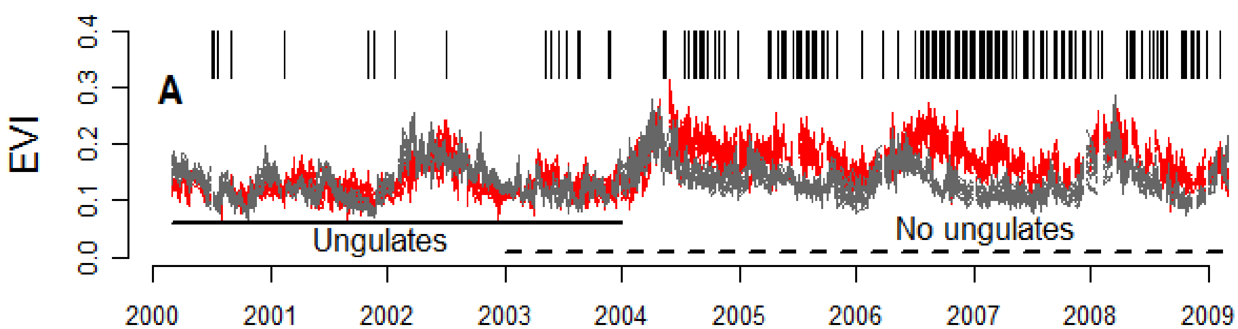

Figure 19. *Time series of satellite phenology between impacted and control sites before and after ungulate exclusion for four years prior to ungulate removal and following exclusion of ungulates. This contrasts a 4.28-km² fenced area (red lines) in which non-native ungulate herbivores were removed and excluded in 2003 (indicated by the transition from solid to dashed lines, just above the axis) with a 3.0-km² control site (gray lines) where ungulate numbers were not manipulated. Solid and dashed horizontal lines overlap because the date when the last ungulate was exterminated is not precisely known. Vertical bars above the data are days when distributions of EVI in managed and control sites did not overlap.*

Even though ERH might explain invasion outcomes between managed and unmanaged MSDF, it cannot explain why some non-native plant species failed to increase following ungulate removal, or why some increased in DVS and MPW. We addressed whether density-dependent population dynamics were contributing to species success by quantifying changes in three functional types. Negative density dependence limited the dominance of forbs, but relationships among C3 and C4 grasses and sedges were weak and marginally significant. This suggests that competition is shaping the local assembly process among species of forbs, because areas with greater forb

dominance had lower realized population growth rates than sites where forbs were rare. We were surprised to discover that there was no significant relationship among C3 or C4 grasses and sedges, because conventional views hold that herbivore browsing suppresses grass dominance (Cabin et al. 2000), and the grass–fire cycle predicts a positive relationship between dominance of grasses and sedges and subsequent changes in cover (D'Antonio and Vitousek 1992). Neither pattern was observed. This indicates that ungulate removal and exclusion did not increase grass dominance at the level of functional types, despite the finding that it permitted increases in non-native species generally. Although ERH can partly explain the increase in exotics in managed MSDF where generalist ungulates were excluded, the large increase in vegetation cover that was observed using satellite observations also coincided with a period of greater than average precipitation. Whether this provides support for some other hypothesis depends on whether exotic success required both enemy release and increased water availability, or only one. Our data suggest that exclusion of feral ungulates (ERH) is the more likely causal explanation for exotic success and invasion of *S. madagascariensis* for two reasons. First, field studies demonstrate that most of the increase in vegetation cover was attributable to exotic plant species, consistent with the prediction of ERH that release from generalists will facilitate the success of exotics more strongly than native species (Keane and Crawley 2002). In the control site where ungulate numbers were not manipulated, fractional cover of exotic plants was 31.3% $\pm$ 2.2% and *S. madagascariensis* was rare, representing just 1.4% $\pm$ 0.5% of fractional vegetation cover. Therefore, precipitation alone was insufficient to facilitate exotic success in the presence of ungulate herbivores. Dispersal limitation is also an unlikely explanation for the absence of *S. madagascariensis* in unmanaged MSDF, because it produces very large numbers of small, wind-dispersed seeds (Sindel and Michael 1988). Second, although ERH predicts the success of exotics in general, and not any one exotic species in particular, the fact that more than half of the increase in exotic plants in managed MSDF was due to one species cannot be ignored. *S. madagascariensis* now represents about 20% of vegetated surface area in ungulate free areas of MSDF, and its functional properties may be expressed in remote observations. At the scale of a MODIS pixel, EVI in low LAI environments is confounded with LAI, lateral vegetation cover, and canopy water content, but is mostly driven by fractional cover changes (Asner 1998, Asner and Vitousek 2005). *S. madagascariensis* is an annual to short lived perennial that experiences cycles of leaf flushing and physiology. It has greater concentrations of leaf water than other plant species during wet conditions, but lower water content during dry periods, and demonstrated capacity to abruptly increase water content. These characteristics were expressed in satellite time series for managed MSDF, but not in control sites where *S. madagascariensis* was rare. Although EVI differences between managed and control sites were maintained after ungulate removal, most differences occurred on days when the landscape was drying (i.e., at times when the slope of EVI time series was negative), but not during green-up events (i.e., at times when the slope of EVI time series was positive. This indicates that effects of enemy release and increases in exotics were expressed mainly during periods of water limitation. The ability of exotics to maintain canopy greenness during dry conditions demonstrates that abundant resources are not a necessary condition for invasion and persistence by enemy release to occur. Whether this is a characteristic of all exotics in managed MSDF or only a subset of species requires further investigation, but it suggests that resource-use efficiency may contribute to the success of *S. madagascariensis* and other exotics. This mechanism has been locally demonstrated for other exotic species in dryland systems of Hawaii (Funk and Vitousek 2007). There are caveats to our interpretation that increases in the dominance of exotic plants in

managed MSDF is attributable to ERH. Our comparison between impacted and control sites is based on two large samples, each of which is replicated through time and separated in space by 18 km. These two areas were chosen because they represent significant portions of the only remaining tracts of MSDF in the world, and because each has inherent conservation value. Nonetheless, because our study is fundamentally unreplicated, there remains a possibility that inherent site differences have confounded the treatment effect and that we have misinterpreted these findings.

In conclusion of this section, the use of Earth observation systems to monitor and assess ecological value has transformed the fields of natural resource management and conservation biology (Turner et al. 2003, Corbane et al. 2015). Now, with some limitation, evaluation of changes in biodiversity, biophysical parameters and ecosystem function can be regularly examined at multiple spatial scales. Further, remote sensing has played an increasingly important role in quantifying ecosystem degradation and conservation-management outcomes towards recovery (see review by Cabello et al. (2012)). For example, remote sensing technology can relate the degrading factors of fire, invasive species and other anthropogenic forces of land use change to biophysical and geomorphic variables, and changes in forest productivity, biodiversity, basal area, tree density, or canopy closure directly convey ecosystem recovery or restoration success (Duro et al. 2007, Vierling et al. 2008, Wang et al. 2009, Calders et al. 2015). In fact remotely sensed estimates of change in forest dynamics are now often adopted as measures of restoration success at community, regional, national and global scales and serve as a foundation for natural resource decision making (Brown et al. 2008).

Findings from this study show how powerful remote sensing tools can be integrated with field studies of tropical dryland ecosystems to confront challenging conservation and management problems. They also provide insight into the mechanisms and historical contingencies that influence non-native invasive species success. Robust planning will require evaluation of competing interests and evaluating the consequences of management action. Removal of non-native feral ungulates is widely considered to be an important first step in conservation and restoration efforts, but its benefits must weighed against the potential cost of subsequent plant invasion if large-scale control is impractical.

4.1.4. Topographic Analysis of Endangered species

The landscape of PTA had 35% of its area in low suitability (LS) (pixel value ¼ 0), 50% in medium suitability (MS) (pixel value ¼ 1), and 15% in high suitability (HS) (pixel value ¼ 2). The class value of all pixels was 0.80 60.01 (mean 6 SE), indicating overall low habitat suitability as defined by our model (Fig. 20). The distribution of classes was similar across substrates of different ages, and HS areas exist across the landscape. The areas currently used by land managers for threatened and endangered species reintroduction had a median pixel value of one and mean pixel value of 0.82. This mean pixel value is similar to the mean of all pixels, indicating that locations used for current reintroductions are not statistically different from a random sample of the landscape.

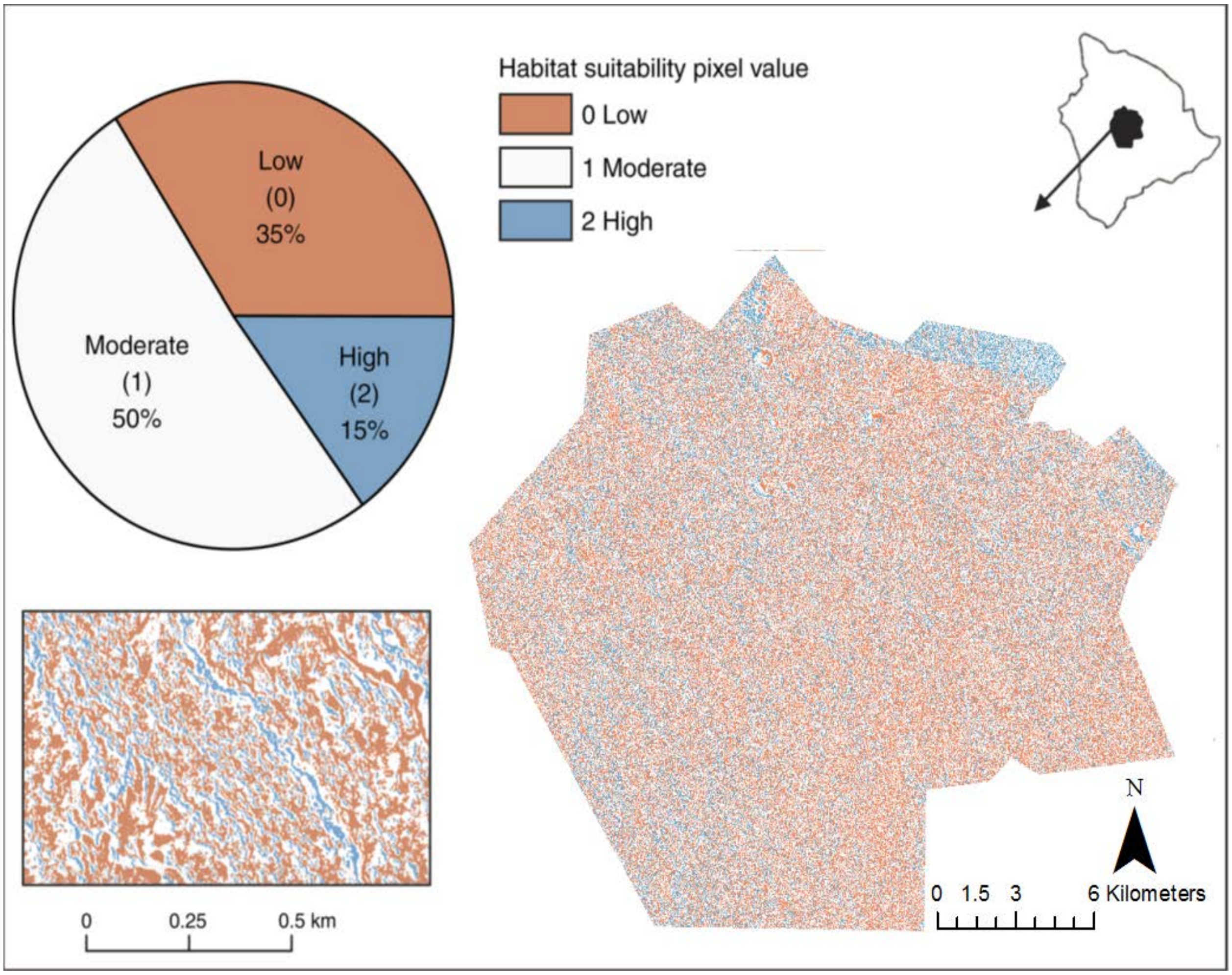

Figure 20. *Habitat-suitability model map for Pohakuloa on Hawaii Island (inset). We based habitat-suitability classes on descending local topography and protection from prevailing winds to model areas with the optimal conditions for plant growth and survival. Pixel values are integers ranging from 0 (low suitability) to 2 (high suitability). The pie chart shows that 35% of the landscape of PTA had pixel values of 0, 50% had values of 1, and 15% had values of 2. The inset in the lower left shows a closer view of an area within PTA and illustrates a typical distribution pattern of the suitability classes at this site.*

Microclimate

Our analysis of microclimatic data indicated differences between suitability classes in conditions that can influence plant growth and performance, with LS sites consistently windier (Fig. 21a), drier (Fig. 21b, c), and relatively deprived of nutrients. Wind speed in the LS plot was over five times higher than in the HS plot (11.8 $\pm$ 0.4 and 2.1 $\pm$ 0.1 km/h, respectively; Fig. 21a). Similarly, maximum gust speed in the LS plot was 66.4 $\pm$ 1.8 km/h compared to 38.7 $\pm$ 1.8 km/h in the HS plot. The number of minutes per day with measurable leaf wetness was higher in HS plots (76 $\pm$ 5.6 min) relative to LS plots (58 $\pm$ 4.0 min; Fig. 21b). The LS plot had more negative water potentials for six of the seven dates measured, indicating less water available to plants. The differences between classes were especially large during dry periods (Fig. 21c). Soil nutrient results were consistent with higher-quality soil conditions in HS, compared to LS, plots. Values for NO3 were higher in HS, compared to LS plots. However, differences between classes were not statistically significant ($P \leq 0.5$).

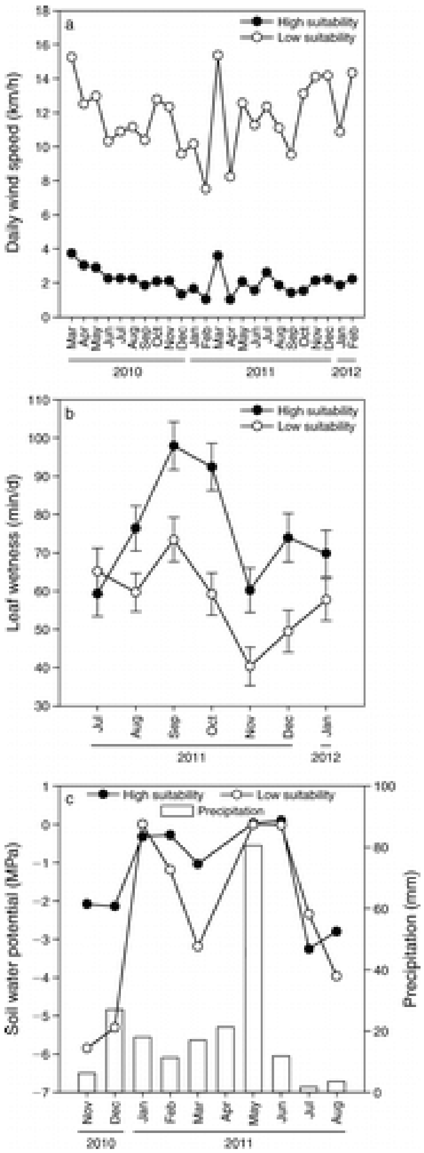

Figure 21. *Microclimate conditions in high- and low-suitability areas. (a) Average daily wind speeds were higher and more variable in the low-suitability, compared to the high-suitability, plot. In both plots, average wind speeds were highest in May and November and lowest in February. (b) The number of minutes per day with measurable leaf wetness was higher in high-suitability relative to low-suitability plots. Values are means ± SE. Leaf wetness differences between the suitability classes were greatest in October during the onset of winter rains and the least in July during the dry season, where leaf wetness was almost identical between the classes. Leaf wetness was highest in the early morning and evening hours with almost negligible leaf wetness measured in both sites between the hours of 08:00 and 14:00. (c) Soil water potential (MPa) was generally higher in the high-suitability, compared to the low-suitability, plot. Each point is a mean of three permanent sampling locations. More negative values indicate drier soil conditions. Bars show total monthly precipitation measured at the site.*

Plant functional traits across suitability classes

The difference in plant height between suitability classes was greatest for the native shrub *D. viscosa* (significant suitability class 3 species interaction; Table 5, Fig. 22a). *D. viscosa* shrubs in HS plots were more than 50% taller than shrubs in LS plots (Fig. 22a). Specific leaf area (SLA) varied among species, but not among HS and LS plots (Table 5). Bars show total monthly precipitation measured at the site. Leaf N was greater in HS than in LS plots for all species (significant suitability class effect; Table 5; Fig. 22b), but the proportional differences among classes varied among species (significant suitability class 3 species interaction; Table 5, Fig. 22b). The native shrub *C. oahuense* had the highest Leaf N among all species in both HS and LS plots, and had greater Leaf N in HS plots (Fig. 22b). The invasive forb *S. madagascariensis* also had a large difference in Nleaf between classes (Fig. 22b). Leaf N did not differ significantly among classes for the other species measured ($P \leq 0.05$; Fig. 22b). Leaf P was greater in HS plots (0.107% $\pm$ 0.004%) than in LS plots (0.090% $\pm$ 0.003%) among all species (significant

suitability class effect; Table 5), differed among species, and there was not a significant suitability class by species interaction. Most of the variation in Leaf C was explained by differences among species (significant species main effect; Table 5).

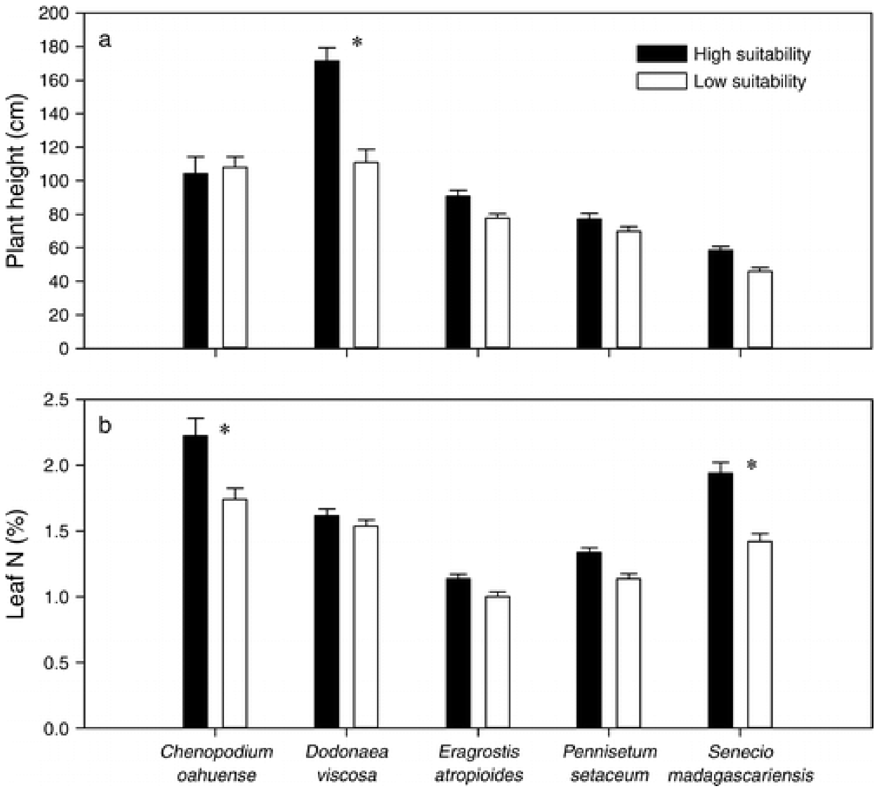

Figure 22. *Plant functional traits of dominant species among suitability classes. Species are native shrubs C. oahuense and D. viscosa, native grass E. atropioides, invasive grass P. setaceum, and invasive forb S. madagascariensis. (a) Plant height and (b) leaf N varied among species and among suitability classes. Asterisks indicate significant differences among suitability classes within each species (Tukey test, P* $\leq$ *0.05). Error bars show* $\pm$*SE.*

Table 5. Test statistic (F) and significance (P) are reported for general linear models of plant functional traits.

	Block			Species			Suitability class			Suitability class × species			
Plant trait	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	R^2
Plant Height	7.67	4, 231	***	8.05	4, 231	*	3.02	1, 231	0.157	10.19	4, 231	***	0.654
ln(SLA)	1.01	4, 260	0.404	63.50	4, 260	***	0.00	1, 260	0.977	0.95	4, 260	0.435	0.519
Leaf N	4.72	4, 229	***	13.60	4, 229	*	11.31†	1, 229	*	5.17	4, 229	***	0.634
Leaf P	11.45	4, 229	***	174.99	4, 229	***	178.71†	1, 229	***	0.09	4, 229	0.986	0.359
Leaf C	8.17	4, 229	***	120.97	4, 229	***	0.05	1, 229	0.828	2.40	4, 229	0.051	0.844

* $P < 0.05$; ** $P < 0.01$; *** $P \leq 0.001$.

† The significant suitability class effect for leaf N and P indicates higher nutrient content in high suitability, compared with low suitability, plots.

Association of threatened and endangered species

We found significant associations between the location of plants and habitat-suitability classes for eight of the 11 species we analyzed. Six species were associated with higher valued classes, and two species were associated with lower valued classes (Table 6). The density of all threatened and endangered plants increased with habitat suitability (Fig. 23).

Table 6. Results of habitat-suitability analysis for existing at-risk species.

Species	Number of individuals	Suitability value of known plants	95% CI of suitability values from simulated populations	Direction of habitat association
Haplostachys haplostachya	11 373	0.9719	0.7542–0.7759	higher*
Hedyotis coriacea	175	0.7257	0.6743–0.8457	no association
Neraudia ovata	41	0.2927	0.5122–0.8537	lower*
Portulaca sclerocarpa	65	0.7231	0.5846–0.8615	no association
Silene hawaiiensis	2 730	0.8048	0.7498–0.7938	higher*
Silene lanceolata	14 607	0.9393	0.7406–0.7594	higher*
Solanum incompletum	154	1.0260	0.6558–0.8377	higher*
Spermolepis hawaiiensis	5 367	0.7593	0.7339–0.7650	no association
Stenogyne angustifolia	2 533	1.1283	0.7165–0.7619	higher*
Tetramolopium arenarium	871	0.5465	0.6349–0.7118	lower*
Zanthoxylum hawaiiense	619	0.7868	0.6801–0.7738	higher*

Notes: We report the mean suitability class value across all known plant points and the 95% confidence interval (CI) of the mean suitability class values of 10 000 simulated populations. All species are listed by the US Fish and Wildlife Service as endangered except *Silene hawaiiensis*, which is listed as threatened. Six species showed an association with higher valued classes, and two species showed an association with lower valued classes. Three species did not show an association.

* $P < 0.05$ for association of the species with either higher or lower classes.

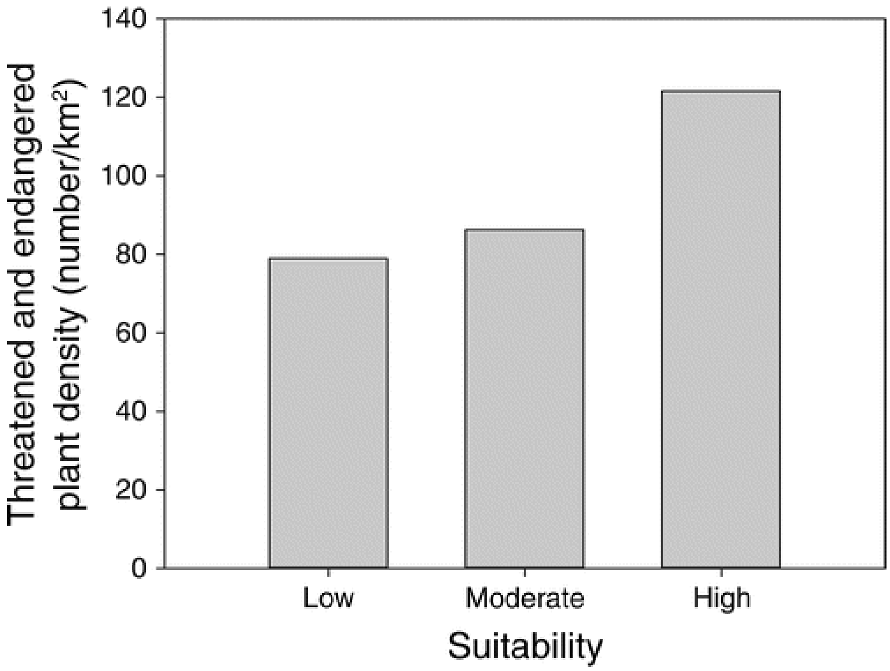

Figure 23. *Density of threatened and endangered plants in each topographic-suitability class. Data are total number of federally listed threatened and endangered plants recorded at PTA divided by the total area of each suitability class at PTA.*

Native outplant survival

There was a trend toward a higher proportion of surviving planted *D. viscosa* in HS plots, compared to LS plots, in July 2011 (HS, 0.93 ± 0.04; LS, 0.78 ± 0.10; one-tailed t test, t = 1.36, P = 0.15), Fall 2011 (HS, 0.85 ± 0.06; LS, 0.57 ± 0.20; one-tailed t test, t = 1.33, P = 0.16), and Spring 2012 (HS, 0.80 + 0.08; LS, 0.57 ± 0.20; one-tailed t test, t = 1.07, P = 0.20). The CV of survival averaged over all dates was significantly lower in HS (0.12 ± 0.02), compared to LS (0.49 ± 0.13) plots (paired t test, t = 3.22, P = 0.04).

Our approach of spatially modeling topographic habitat suitability can inform plant reintroduction and restoration programs in dryland ecosystems. The high spatial resolution of our data made it possible to model topographic features that are important to the establishment and growth of small, low-statured plants; and the extensive nature of remote sensing data allow for large-scale analysis useful for planning at the landscape level. Further, our field analysis of the HSM provided several lines of evidence that support its use to guide restoration and reintroduction programs. High-suitability habitats had (1) more favorable microclimate conditions important for regeneration, (2) plants that showed greater growth and resource capture through measured functional traits, and (3) lower variability in survival rates of planted *D. viscosa* seedlings. The HSM can improve restoration success by guiding planting activities to areas of the landscape with favorable microclimates that reduce plant stress and decrease variability in survival among planting locations.

Water stress is the primary barrier to plant growth and survival in this and other dryland ecosystems, and the sites that we identified as high suitability had microclimatic conditions associated with reduced water stress. Annual precipitation is low (400 mm) and the porous volcanic substrate does not store water for long periods following rain. In addition, wind speeds are high with gusts typically from 60 to 90 km/h, which create conditions of high evaporative demand for plants. During several periods, soil moisture and leaf wetness of high-suitability areas were greater than low-suitability areas. Periods of higher leaf wetness are possibly associated with moisture inputs from fog, which can be a significant source of water during dry conditions (Dawson 1998, Liu et al. 2004, Liu et al. 2010). The dramatic decline in wind speeds in the high-suitability site may be one of the most effective ways our model can reduce water loss through transpiration (Fig. 2a). This reduction in transpiration stress may be why other studies have found higher restoration and reintroduction success on the leeward sides of topographic features (Pipoly et al. 2006, Biederman and Whisenant 2011, Simmons et al. 2012). We can significantly reduce wind related water stress by using the HSM to position reintroduced plants in highly suitable sites that are protected from prevailing winds by existing topographic features. Our analyses of plant responses to the HSM further support the use of this approach to guide reintroduction efforts. The functional traits of plants we measured in the field indicated that high-suitability sites support greater plant growth and performance. Plant functional traits represent the evolved attributes of species, ecologically driven trade-offs, and the effect of species on ecosystem processes (Lavorel and Garnier 2002). They are often measured to indicate differences in life history trade-offs among species (e.g., competition– colonization trade-offs between growth and seed size); however, they may also indicate responses to environmental gradients (Lavorel and Garnier 2002, McGill et al. 2006). We observed greater Leaf N and Leaf P averaged over all species in high-suitability, compared with low suitability, sites, which may reflect higher soil nutrient availability. The height of three species was greater in high-suitability, compared with low-suitability, sites, suggesting that these species have greater resource acquisition and productivity in high-suitability areas (Weiher et al. 1999). Six of the existing populations of threatened and endangered plant species had individuals that were associated with higher-suitability sites, and more threatened and endangered plants occurred in high-suitability areas (Fig. 23). The preliminary results from our experimental planting of *D. viscosa* seedlings showed less variability in survival of planted individuals among plots in high-suitability areas and a trend toward greater survival in high-suitability sites. Together, these results provide strong support for using the HSM to guide plant restoration and reintroduction efforts.

Management implications

LiDAR is an important tool for mapping habitat suitability for at-risk species. Its high spatial resolution (i.e., small ground sampling distance) allows for mapping small features of the landscape that are important to many organisms (e.g., soil depressions, heterogeneity of forest canopy structure). The large spatial extent of remote sensing data provides insight across significant portions of the range of many species and generates data useful for conservation decisions at landscape scales. Most applications of LiDAR in this manner use data of vegetation structure to map habitat quality for terrestrial wildlife species or to understand forest stand structure more generally (Dubayah et al. 2000, Lefsky et al. 2002, Turner et al. 2003, Vierling et al. 2008, Hudak et al. 2009). The most similar LiDAR analysis to our study linked the species richness of a tropical forest community to terrain elevation and curvature (Wolf et al. 2012). Species richness was greater at lower elevations and in concave, compared to convex, terrain features (Wolf et al. 2012). These features generally indicate areas with greater soil moisture in this ecosystem (Daws et al. 2002), suggesting that plant diversity was greater in areas with greater soil moisture. This finding is in accordance with our results of greater soil water potential and plant resource acquisition in topographic depressions. Several studies have used LiDAR topographic data to model three-dimensional features in aquatic ecosystems (Jones 2006, James et al. 2007, Hogg and Holland 2008, Knight et al. 2009). Jones (2006) used LiDAR topography and orthoimagery to model habitat suitability for salmon restoration planning and concluded that the cost of restoration projects could be reduced by using their data to identify suitable areas and minimize the need for field inspections. Our habitat-suitability model (HSM) can also be used in a similar way to minimize costs of plant reintroduction projects. In addition, our study is the first to our knowledge to employ LiDAR in the context of using high resolution imagery to define areas of the landscape for native plant restoration.

The HSM can redefine habitat restoration and at-risk plant reintroduction programs by providing a set of quantitative, spatially explicit tools to increase the success of planting efforts. Variability in survival rates among planting sites is currently a major challenge to reintroduction projects, including those at our study site (Godefroid et al. 2011). The significant reduction in variability (lower CV) that we observed in the survival of *D. viscosa* outplants and the trend toward greater overall survival in high-suitability areas supports the use of the HSM to overcome this challenge. *D. viscosa* is the most commonly used native species in habitat restoration plantings due to its importance as a dominant species in this ecosystem, its capacity to grow fairly quickly, and its ability to withstand some fires. Thus, we are optimistic that our HSM can improve the success of native habitat restoration activities. The current survival rate of threatened and endangered outplants at PTA is highly variable among species and sites (15–73%; K. Kawakami, unpublished data). Outplanting sites at PTA are arbitrarily selected, and had relatively low suitability values. We expect an increase in survival if our HSM technology is employed; however it is not yet clear how broadly we can apply this HSM across species. The two herbaceous species we tested (*Portulaca sclerocarpa* and *Spermolepis hawaiiensis*) did not show an association with our habitat suitability classes. The six species that were associated with higher-suitability areas are perennial woody plants. It is possible that the HSM will be most useful for reintroduction activities for woody species, but further study is needed to determine how individual species will respond. However, an increase in survival of any species that result from using the HSM would help reduce the costs of reintroduction programs. An additional benefit of the HSM is the improved ability to make management decisions at landscape scales.

The management of at-risk species in most ecosystems is extremely expensive and labor intensive. Management activities such as fire suppression, removal of nonnative herbivores, and control of invasive plant species are often more expensive to maintain than planting programs because they require a large up-front investment of labor and materials and constant maintenance. Management is also challenging in areas like PTA that are large and difficult to access due to having few roads, rough terrain, and military training activities. The HSM can be used to select regions of the landscape with a large amount of high-suitability habitat for intensive, expensive, management activities. It can also help managers identify nearby parcels for acquisition or conservation easements that may have a high value for threatened and endangered species recovery and mitigation activities. Therefore, this tool will be especially effective in regions that are difficult to access due to their remote location or lack of infrastructure.

We believe this modeling approach will be useful in many other areas, especially in other dryland ecosystems. However, a DEM with high spatial resolution ($\leq$ 2.5 m) is necessary for modeling fine-scale microtopographic features that are important for plant growth. Our DEM was derived from airborne LiDAR measurements from the CAO, which are not widely available, and the cost of airborne LiDAR data acquisition can be limiting. Satellite data sources now exist that that may provide some degree of precision for mapping topography at high resolution (1–5 m). Stereographic DEMs from satellites such as World-View-2 are globally available, so they can be used to generate HSMs anywhere in the world. Sensors flown on lightweight unmanned aerial vehicles could also provide a cost-effective method to generate DEMs with high spatial resolution (Anderson and Gaston 2013). As these technologies develop and become cost effective, they offer the possibility of expanding the HSM tool to other regions with active reintroduction programs. We are excited by the potential to use the HSM in other critical conservation areas. We have explored numerous lines of evidence that all support our initial hypothesis that topographic depressions that are protected from wind are more favorable habitats for plant growth and regeneration. Our study is unique in that we combine a remote modeling approach with extensive field measurements of microclimate conditions and plant functional traits, and a planting experiment. The HSM should be field validated in a similar way if it is used in other locations, and we hope that if other managers adopt this approach, recovery efforts for at-risk plant species will have greater success.

4.1.5. Remote Sensing Tools for Restoration

Where important ecological processes are intact, restoration may be as simple as controlling above- or belowground harmful invaders. In more degraded ecosystems, however, an understanding of basic ecological processes and the constraints that altered the present ecosystems is fundamental to restoration success (Suding et al. 2004, Suding et al. 2013). Further, the landscape where we work supports a dynamic social-ecological setting because communities and ecosystems in Hawaii are small, compressed in scale, and close knit, and where multiple stakeholder interests can produce conflicting perspectives on restoration. In the PTA case study, stakeholder interests include mandated protection of threatened and endangered species and their associated habitat, military training, public recreation (hunting), and public safety (wildfire).

Given that the land represents a very limited resource, it is important to recognize its potential and optimize its usage via an objective and quantifiable approach. The most overt challenge in this ecosystem is between protection of biodiversity and public hunting of non-native animals. Threatened and endangered species can likely only persist in areas protected from non-native animals (Cole et al. 2012), but these same animals depend on forested habitat. Complicating these opposing interests, federally-mandated critical habitat for threatened and endangered species generally encompass large areas of historical habitat, forcing land managers to protect vast tracts of land for potential species recovery. This strategy is problematic because much of the landscape has been so altered and degraded that native species recovery is virtually impossible. This policy reduces other land use activities such as military training opportunities and hunting areas, thereby fueling a long-lasting and currently unresolved debate.

To address these complex dynamics our approach was to use high-resolution remote sensing tools to identify areas of the landscape where stakeholder activities can be prioritized based on biophysical and geomorphic characteristics. Using this approach we anticipate that areas deemed high priority for restoration can be more intensively managed, thereby releasing low priority areas for recreation and military training. In addition, areas with high risk of fire can be targeted for appropriate fire reduction activities.

Description of mapping tools

Our overall goal was to develop restoration planning tools for the PTA region that reflect different stakeholder interests. First, we created map layers of *restoration potential* and fire *fuel accumulation* for the 49,000 ha PTA installation using LiDAR and spectroscopic measurements from the Carnegie Airborne Observatory (CAO) (Asner et al. 2007). We then combined the layers to identify areas of the landscape where different stakeholder interests could be met. Third, we used NASA MODIS satellite data to develop a tool to monitor near real-time fire fuel conditions to provide additional assistance with fire management (Figure 24).

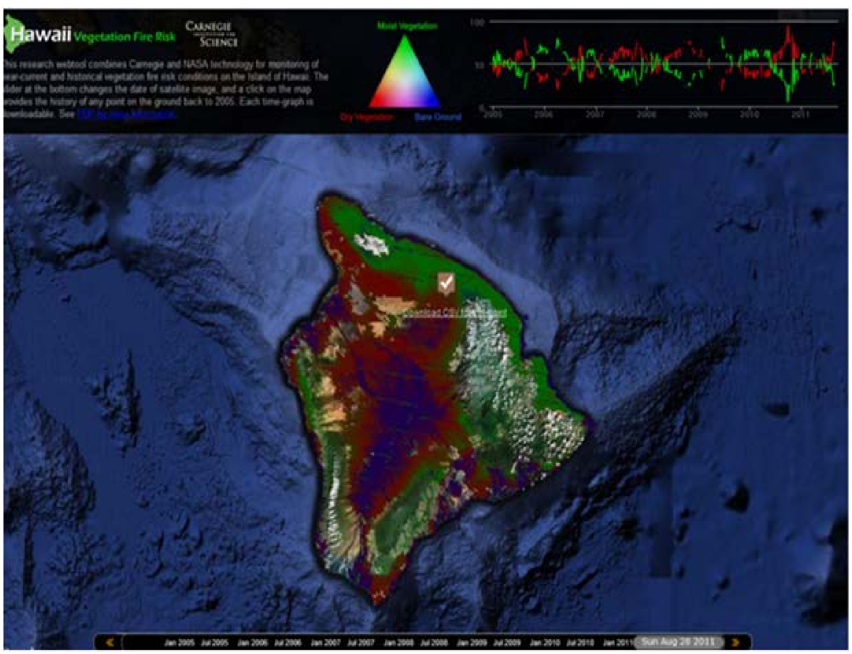

Figure 24. *User interface of the web-based fire fuel monitoring system that combines Carnegie and NASA technology for monitoring of near-current and historical fire risk conditions on the Island of Hawaii. The glider at the bottom of the screen allows the user to change the satellite date of the image and a click on the map provides the history of any point on the ground back to 2005. Each time-graph is downloadable.* (http://hawaiifire.stanford.edu)

Here, we present examples of our approach from two plant communities, a shrubland dominated by *Dodonaea viscosa* and a forest dominated by *Metrosideros polymorpha*.

We wanted our maps of *restoration potential* to show areas of the landscape with microclimates that will promote plant growth and establishment during restoration. We used LiDAR data to derive a digital terrain model (DTM) of the ground and a digital surface model (DSM) of the vegetation canopy (for methods see Kellner et al 2011). The ground sampling distance, or pixel size, of these models was 2.2 m. This fine-scale mapping allowed us to model relatively small features important for plant growth and establishment, including the microtopography and individual trees. We defined restoration potential in the *Dodonaea* shrubland using the DTM to identify topographic features that can improve plant establishment (Questad et al. 2014). Areas with high restoration potential met two criteria: (i) they are in topographic depressions; and (ii) they are protected from the prevailing winds by an existing topographic feature (Fig. 25). Areas with high restoration potential were found to be more suitable for plant establishment and growth (Questad et al. 2014). High restoration potential in the *Metrosideros* forest was defined as areas with more canopy cover. Canopy cover reduces solar radiation and wind exposure to restored seedlings, and should improve plant establishment compared to more open, exposed (Uhl and Kauffman 1990, Freifelder et al. 1998, Scowcroft and Jeffrey 1999). We used the LiDAR-based DSM to calculate the density of pixels with canopy greater than 2.5 m in height (e.g., trees) in a 22 m x 22 m area (10 x 10 pixels in the DSM). Areas that we defined as having high restoration potential had canopy cover in the top 10% of the distribution across the *Metrosideros* forest (Fig. 26a). These areas contained 28-87% tree cover.

Our maps of *fuel accumulation* focused on fine, fire-prone fuels because fires in Hawai'i are driven mainly by invasive grasses (Smith and Tunison 1992). The abundance of standing, senescent biomass is the main source of fuel from these perennial grasses. We modeled these fuels using spectroscopic measurements and LiDAR data from the CAO to quantify the fractional abundance of non-photosynthetic vegetation (NPV) less than 2m in height (Asner and Lobell 2000, Varga and Asner 2008). Values in the upper 10% of the distribution of pixels in each study area were considered as areas of greatest fire risk (Figs. 25b, 26b). Areas in the shrubland and forest with the greatest fuel accumulation had 51.6% and 40% cover of NPV, respectively (Kellner et al. 2011).

The map of *fuel accumulation* lets us compare relative abundances of senescent biomass in a spatial context (i.e., from one area to another in the landscape); however, the growth and senescence of perennial grasses is a dynamic process occurring throughout the year. We mapped fuel conditions using data from the MODIS sensor, which provides sufficient spectral information on an 8-day repeat cycle to allow for coarse-scale temporal modeling (Elmore and Asner 2006). The data are limited to 250 m ground sampling distance, thus they serve only as a broad indicator of fire hazard conditions. Nonetheless, this modeling technique corresponds with both aircraft and field-based measurements of dry fuel cover and moisture content (Elmore and Asner 2006). This product is available as a web tool, and has been effectively introduced to the U.S. Department of Defense (DoD) and other Hawaii-based land managers (http://hawaiifire.stanford.edu) (Fig. 24). This product combined with the one-time high resolution *fuel accumulation* map provide the most complete understanding of spatial and temporal variations in fuel conditions in this region.

We combined the maps of *restoration potential* and *fuel accumulation* to identify areas of the landscape where particular restoration activities are likely to be the most effective. For example, **physical fire barriers** such as fuel breaks cleared of vegetation can be targets in areas with high fire risk and low restoration potential (Figs. 25c, 26c). There is also interest in using native plant restoration to reduce fine fuels (green fuel breaks), by increasing the abundance of native shrubs to exclude invasive grasses. This type of **ecosystem process-level restoration** could be the most effective in areas with high fire risk and high suitability for plant growth (Figs. 25c, 26c). In addition, the MODIS fuel monitoring tool provides information that can help plan management activities throughout the year. For example, fuel breaks can be inspected and expanded during times of high fuel accumulation, and areas focused on ecosystem process level restoration can be monitored for fire risk during these times. **Restoration of endangered plant populations** through intensive management and reintroduction can be focused in areas with low fire risk and high restoration potential (Figs. 25c, 26c). These areas would have the best microclimatic conditions for successful outplanting and would have the lowest risk of losing the plants to a fire. Based on location data from non-native ungulates that were tracked and monitored with radio collars (Chynoweth et al. 2015), we found that non-native ungulates were more likely to occur in areas with high suitability for restoration compared to other areas; however, they also commonly occurred in areas with moderate suitability (Fig. 27). These animals could be managed for **recreational hunting** in areas with moderate suitability because areas with high suitability are limited and are extremely important for restoration and endangered plant conservation (Questad et al. 2014). The landscape contains a larger area of moderate suitability than high suitability, which would create flexibility in where hunting reserves could be located.

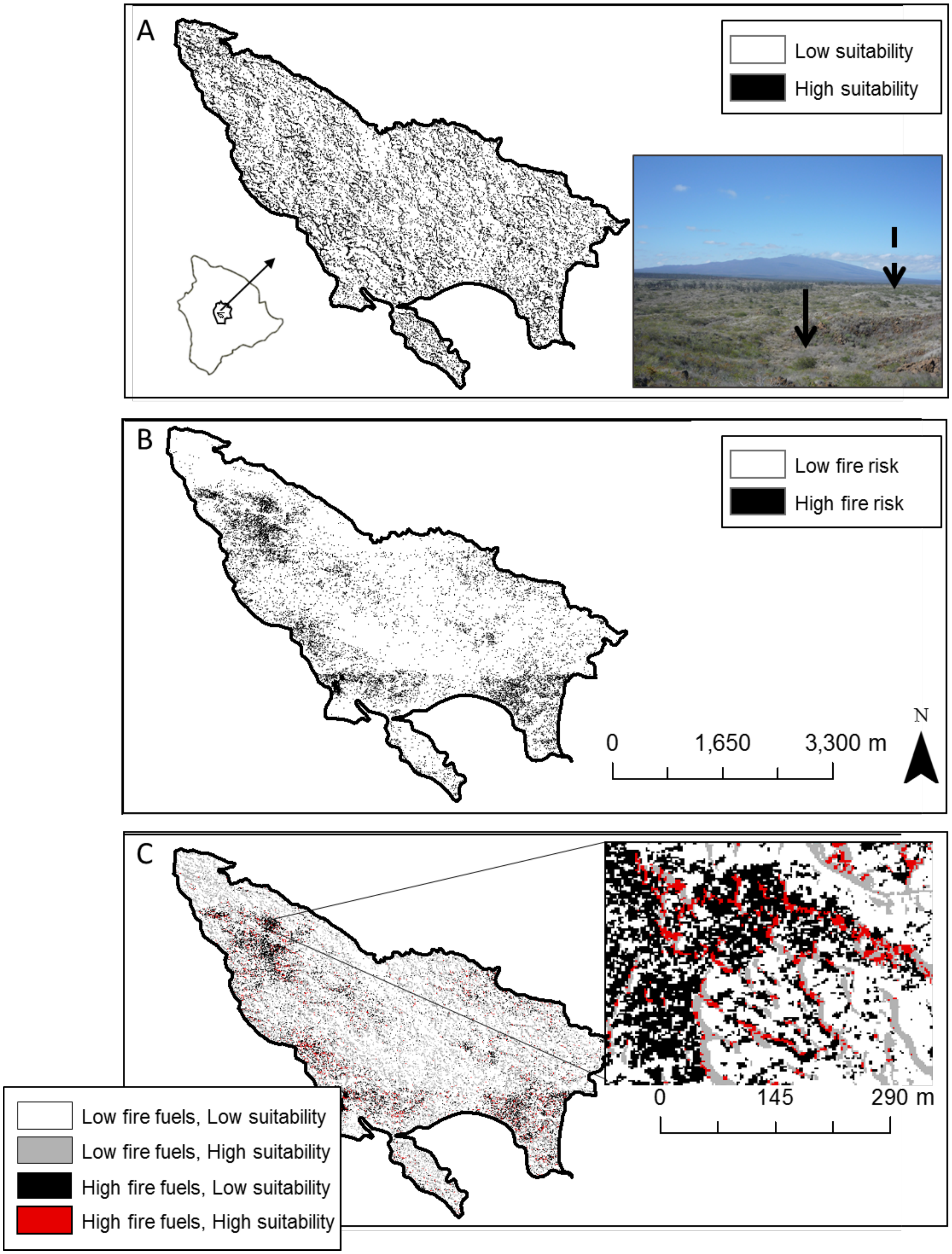

Figure 25. *Restoration potential maps of the Dodonaea viscosa shrubland at PTA. A) map of suitability for restoration based on microtopography, the photo illustrates an area of high suitability with a solid arrow and low suitability with a dashed arrow; B) map of fire risk based on the accumulation of fine, flashy fuels (NPV < 2 m in height); C) map combining A and B to assist with decision-making.*

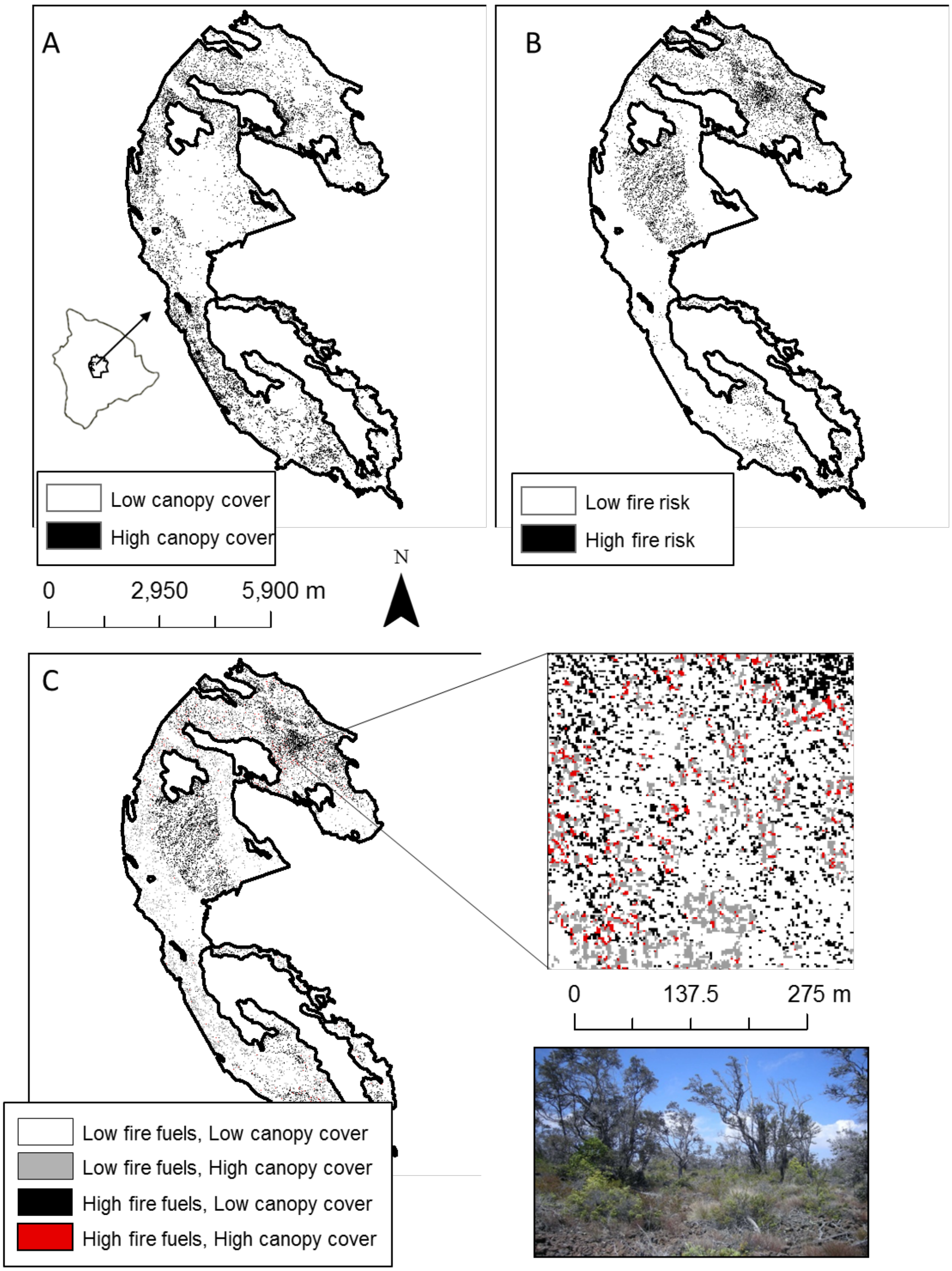

Figure 26. *Restoration potential maps of the Metrosideros polymorpha forest at PTA. A) map of suitability for restoration based on canopy cover; B) map of fire risk based on the accumulation of fine, flashy fuels (NPV < 2 m in height); C) map combining A and B to assist with decision-making.*

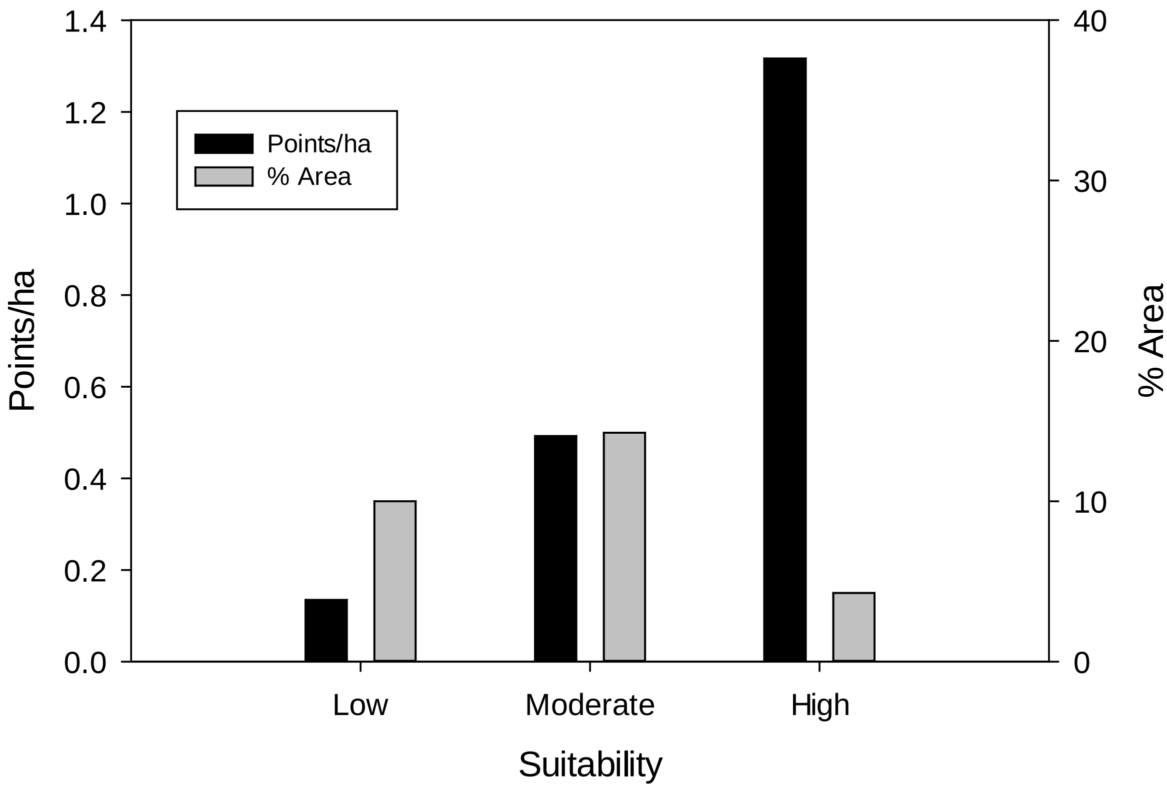

Figure 27. *Location points of invasive goats at PTA. Black bars show the number of occurrence points per hectare in high, moderate, and low suitability for restoration classes recorded from 8 July to 30 December 2010 on 11 animals. Grey bars show the percentage of each suitability class in the PTA landscape. Goats were located more often in high suitability areas despite the low abundance of these areas in the landscape.*

Conclusion

This comprehensive approach has provided basic scientific information and practical tools for managing and restoring this Hawaiian landscape while meeting the needs of multiple stakeholders. Results benefit natural resource managers by increasing capacity and knowledge to restore native ecosystems, thereby reducing wildfire and meeting resource management goals. This process also allows land managers to allocate resources, make land use decisions using a quantitative approach to increase the likelihood of success, and reduce conflict between multi-use stakeholders. By combining strong spatial (e.g., airborne LiDAR) and temporal (e.g., spaceborne MODIS) observations, managers can effectively monitor outcomes of on-the-ground activities, track responses to interannual variations in climate, and reduce stakeholder tensions. For example, mandated restoration of high-value species and associated habitat should be focused in the highest suitability areas, which also represent the lowest percentage of the landscape. Conflicts with the hunting community could be alleviated by allowing non-native ungulates to utilize portions of the land of moderate suitability (Fig. 27). In addition, military installations in Hawaii and the Pacific are responsible for the protection of approximately 120

threatened and endangered (T&E) species (~20 % of the species in the US) thereby providing a significant service to the protection of biodiversity, but at a cost towards their mission (Stein et al. 2008). Effectively partitioning the landscape for focused management activities in the areas of highest conservation value could substantially increase capacity and reduce budgets by focusing training in lower quality areas. Finally, remotely sensed fuel data can be linked with other sources of data such as road layers and/or wind speeds to better prioritize fuels management activities.

In this case study, we set thresholds for defining areas with high fuel accumulation and high restoration potential. For example, we defined high fuel accumulation as the top ten percent of the distribution of fuel values. This type of threshold is flexible, and can be changed to meet different management goals. If more resources become available we could set the threshold lower to define a larger area for management. Likewise, if we know the specific requirements of a species of concern we can use the data to define its habitat, such as locating areas of completely intact tree canopies for a plant species that grows only in a closed canopy. Thus, the maps we present here are just one example of how the data can be used to visualize a landscape. Each restoration project will have to consider the tradeoffs between data quality, area covered, and cost (Table 7). In our case, we used airborne hyperspectral and LiDAR remote sensing, which produce data-rich but costly results. However, the MODIS data we used for the near real-time fire map are free to end-users. For smaller restoration projects, UAVs may provide a low cost platform for collecting useful data. UAVs are now inexpensive and ubiquitous and can collect data to help with setting up plots, creating planting plans, delineating key features such as wetlands, and monitoring projects post-restoration. Cost versus quality decisions will always be an important part of the discussion for restoration of large landscapes.

Beyond this case study the potential for using remotely sensed data in restoration projects is promising. Once stakeholders identify limiting factors and barriers to restoration an appropriate scale and tool can be applied. For example, in tropical wet forests light availability in the forest can be effectively mapped and targeted using spatial data on canopy gaps and/or calculated values of leaf area index (LAI), while temporal data can efficiently document change over time or effectiveness of restoration treatments or management activities. High-resolution digital elevation models can be used to detect subtle variations in slope or aspect or unique micro topographic features relevant to restoration such as small depressions, wetlands or vernal pools. Many of these features are not easily detected using traditional methods.

Results from this case study show the potential of using remote sensing tools in ecosystem restoration to increase capacity and knowledge to restore ecosystems through wildfire reduction, protection of high value habitats, and conflict resolution between multi-use stakeholders. This work could potentially re-define the way land managers accomplish multi-use missions on their landscapes by providing a set of quantitatively based and spatially explicit tools to ensure effective and compliant land use management.

Table 7. Comparison of tradeoffs for different types of remote sensing data and applications for restoration.

	Pixel Size	Frequency	Spectral Resolution	Cost	Data Products useful for Restoration	Restoration Applications
Airborne sensor	50cm - 5m	Single image	Low - High	$$$	Detailed topography or vegetation mapping of a specific area	Site selection, Identifying features
Landsat http://landsat.usgs.gov	15 - 100m	16 days	Moderate	$	Measures of vegetation "greenness"	Larger-scale monitoring of restoration projects, Monitoring plant invasions
MODIS http://modis.gsfc.nasa.gov	500 – 1000m	8 days	Moderate	$	Measures of vegetation "greenness", Evapotranspiration, Recent fires	Larger-scale monitoring of restoration projects, Monitoring plant invasions
UAV	10 - 100cm	Single image	Low - High	$-$$	Detailed topography or vegetation mapping of a specific, small area. Flexibility for repeated sampling at low cost	Site selection, Identifying features, Restoration monitoring, Monitoring plant invasions in a small area

4.1.6. Web-based Satellite Monitoring

In a basic sense, fire is fueled by dead vegetation and altered by live vegetation. However, once a fire is ignited, live vegetation often forms part of the fuel bed. Because of this, a ratio of live cover (PV) to total cover (PV + NPV) is important. This ratio provides information both about the fire 'damping' effect that the live vegetation causes, as well as information about the total possible available fuel. Fraction of Live Cover (FLC) is calculated for each pixel:

$$FLC = PV / (PV + NPV)$$

There are numerous locations on the Big Island that experience grass fires; these locations are not constrained to one climatic or biological zone. These differences correspond to varying fuel bed conditions (such as different grass species). Because of this, one measure of fuel condition is not relevant across the entire island. Instead, we plan to scale the observed Fraction of Live Cover of each pixel to the range of historical FLC values for that one location:

$$FC = 1 - (FLC_{max} – FLC_{observed}) / (FLC_{max} – FLC_{min})$$

This provides us with a Fuel Curing Index, scaled between 0 and 1, with high values corresponding to a historically low fraction of live cover (i.e. high fire potential). The Fuel Curing Index provides general information about the quality and quantity of fuel in any given area throughout the year, can be based retrospectively on the MODIS record from 2000-2006,

and can project in near real time via the web. The data are limited to a 250 m pixel size or ground sampling distance, thus they serve only as a broad indicator of fire hazard conditions. Nonetheless, this modeling technique corresponds with both aircraft and field-based measurements of dry fuel cover and moisture content (Elmore and Asner 2006). This product is available as a web tool, and has been effectively introduced to the U.S. Department of Defense (DoD) and other Hawaii-based land managers (http://hawaiifire.stanford.edu). This product, combined with the one-time high resolution *fuel accumulation* map (Fig. 26b) provides the most complete depiction of spatial and temporal variations in fuel conditions in this region.

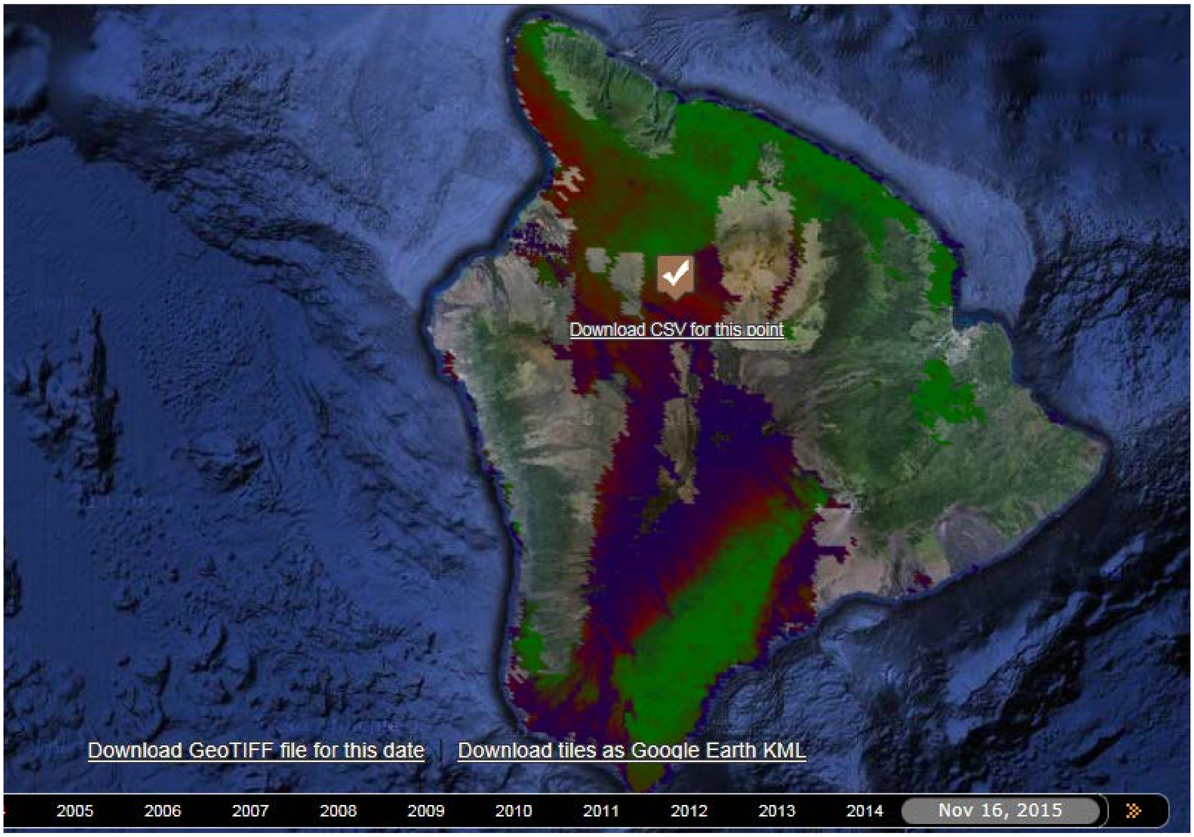

Figure 28. *User interface for downloading time-graphs of the web-based fire fuel monitoring system that combines Carnegie and NASA technology for monitoring of near-current and historical fire risk conditions on the Island of Hawaii.*

4.2. Field Based Studies

4.2.1. Restoration Experiment in Remnant Forests and Shrublands

Restoration Experiment

Our experimental design (Fig. 6) allows us to assess the effects of restoration on fuels in two ways. First, by comparing initial differences in fuel and microclimate conditions between plots with degraded and suitable habitat, we can quantify effects of canopy trees and topographic position on fuels. Secondly, we can assess restoration effects by monitoring changes that occur

as we increase native cover in the forest understory. This approach will allow us to not only determine ecosystem specific restoration prescriptions, but to also help effectively guide resources towards breaking the grass/fire cycle.

The effectiveness of restoration treatments were measured as native plant survival, increases in native species cover, decreases in fuel loads and changes in microclimate. A main finding is that the effect of habitat suitability and restoration treatments on measures of restoration effectiveness varied across sites, suggesting that restoration prescriptions are site-specific and cannot be generalized. For example, weed removal increased survival of the first cohort of outplants at the Shrubland site, but it had no effect on survival at Puu Waawaa or at Kipuka Alala (Fig. 3). Weed removal reduced the survival of the second cohort of outplants at Kipuka Alala, and increased the survival of outplants at Puu Waawaa. Habitat suitability affected survival of outplants at the Shrubland site, where habitat suitability was based on topography; however habitat suitability based on canopy cover did not significantly affect survival at Kipuka Alala or Puu Waawaa.

Effects of treatments also varied for grass fine fuels. The live:dead ratio of grass biomass is an indicator of flammability. Weed control reduced the live:dead ratio of grass biomass at the Shrubland and increased the live:dead ratio of grass at Puu Waawaa. In addition, dead, live, and total biomass were higher in high suitability plots at the Shrubland, but canopy cover did not affect any measure of fine fuels.

Experimental effects on native cover also varied among sites. Kipuka Alala had the highest native cover of all of the sites before treatments were administered. As a result, there were not strong effects of the treatments on increasing native cover. For example, high suitability plots had higher native cover compared to low suitability plots mainly due to the presence of native shrubs in high suitability plots before restoration (Fig. 11b). In the Shrubland, native cover was higher in high suitability habitats and higher when weeds were controlled most likely due to the higher survival of restored native plants in these areas (Fig. 13). Outplanting and habitat suitability had the greatest effects on native cover at Puu Waawaa most likely due to the much higher growth of outplants at this site, compared to the sites at PTA.

Overall, habitat suitability and weed control had a strong influence on restoration success at the Shrubland site, there were not strong effects of restoration treatments at Kipuka Alala, and outplanting and weed control were effective at Puu Waawaa. Thus, previous research using outplanting in lowland dry forests may not apply directly to the restoration of subalpine dryland ecosystems.

Outplant survival

Survival of the first cohort of seedlings was significantly different among sites (Fig. 29, one-way ANOVA, $F_{2, 1377} = 278.53$, $p<0.001$). All sites differed from each other (Fig. 29, $p<0.001$). Survival at KAA was low overall. The Date factor was significant for KAA due to higher survival following outplanting. Aweoweo had the highest survival at the PWW and SHRUB sites (Fig. 30). Weed removal ($F_{1,479} = 8.84$, $p=0.003$), species ($F_{7,479} = 15.13$, $p<0.001$), and date ($F_{4,479} = 15.33$, $p<0.001$) affected survival at the shrubland site. Species and Date affected survival at PWW (Fig. 30). Weed removal increased survival at the shrubland site, but not at PWW (Fig. 31).

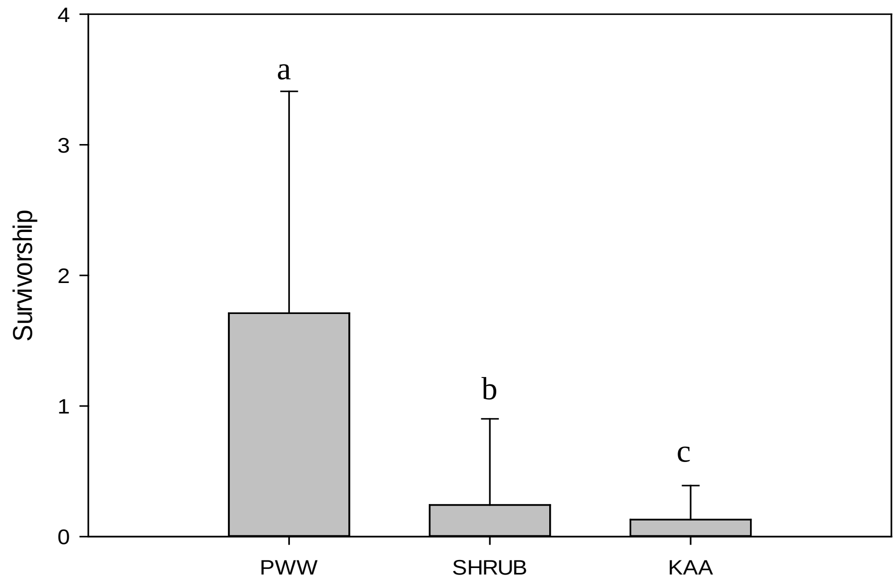

Figure 29. *Survivorship of all outplants (first outplanting) across sites. Error bars show 1SD.*

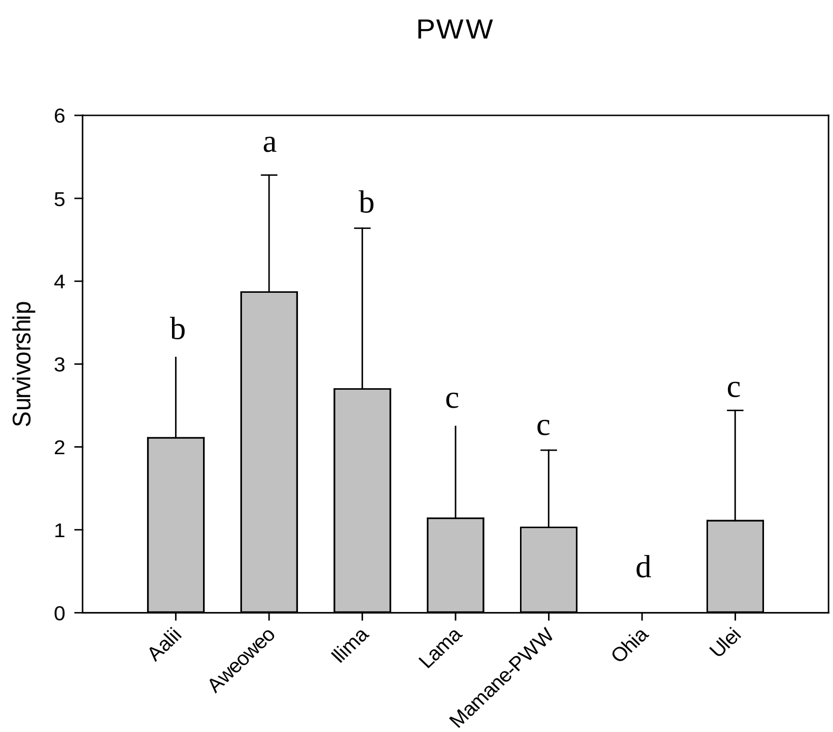

Figure 30. *Survivorship of outplants (first outplanting) at PWW as a function of species. Error bars show 1SD. Letters indicate statistically different means, P <0.05*

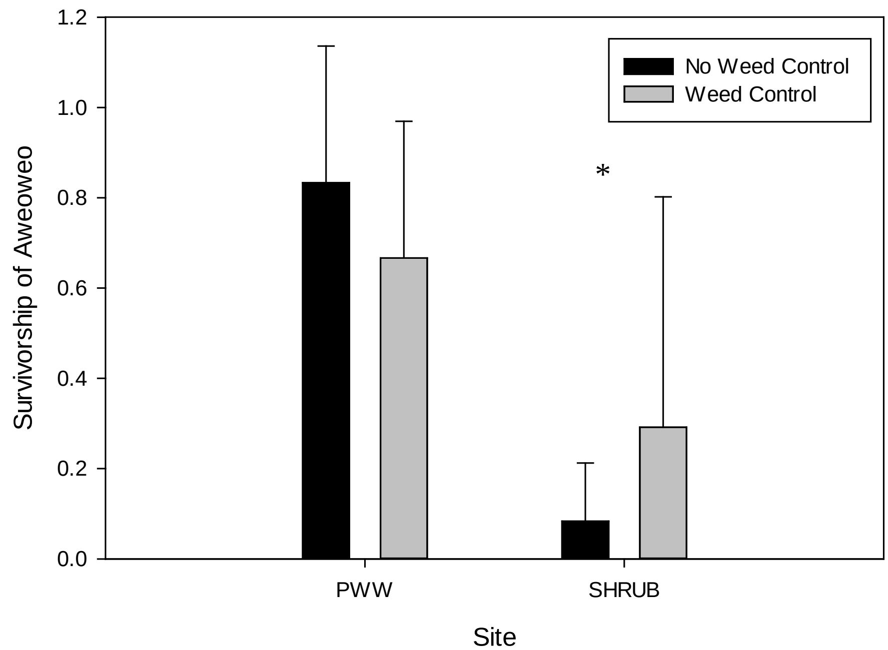

Figure 31. *Survivorship of Aweoweo outplants (first outplanting) among weeding treatments at the PTA shrubland and PWW. Error bars show 1SD. *P<0.05*

Survival of the second cohort of *Dodonaea viscosa* seedlings was significantly different among sites (one-way ANOVA, $F_{2, 81} = 23.20$, $p<0.001$; Fig. 32). Survival was higher at the KAA and Shrubland compared to PWW (Fig. 32, $p<0.05$). The weed removal factor was significant at KAA because survival was lower in weed removal plots (Fig. 33; $F_{1, 19} = 10.57$, $p=0.004$). Weed removal was significant at PWW because survival was higher in weed removal plots (Fig. 34; $F_{1, 19} = 6.63$, $p=0.019$). Habitat quality affected survival at the shrubland site (Fig. 35). Survival higher in high, compared to low, suitability habitats. Habitat suitability (canopy cover) did not significantly affect survival at PWW or KAA.

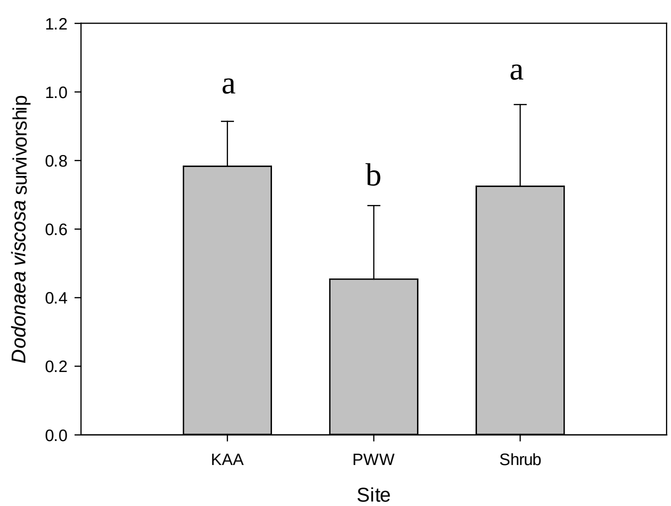

Figure 32. *Survivorship of Dodonaea viscosa outplants (second outplanting) across sites. Error bars show 1SD. Letters indicate statistically different means, P <0.05*

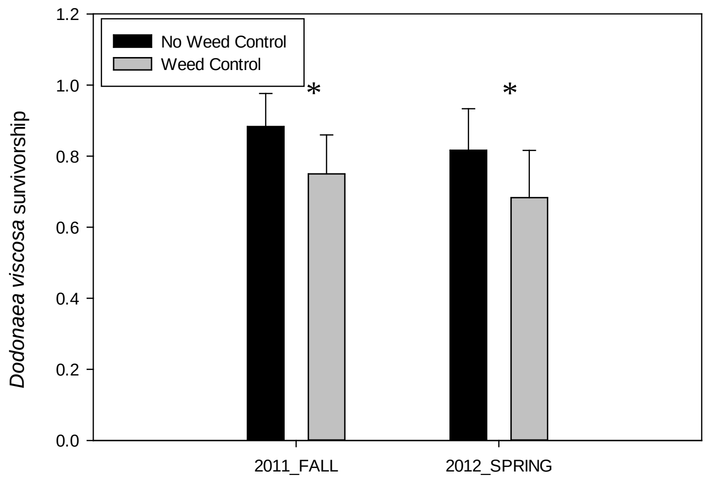

Figure 33. *Survivorship of Dodonaea viscosa outplants among weeding treatments at KAA. Error bars show 1SD. *P<0.05*

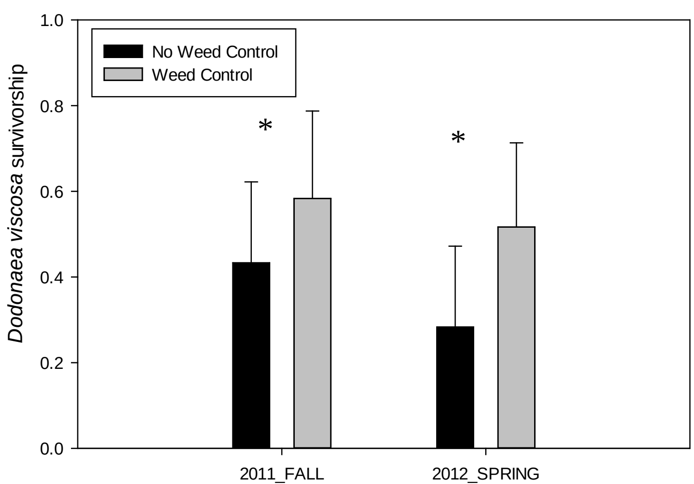

Figure 34. *Survivorship of Dodonaea viscosa outplants among weeding treatments at PWW. Error bars show 1SD. *P<0.05*

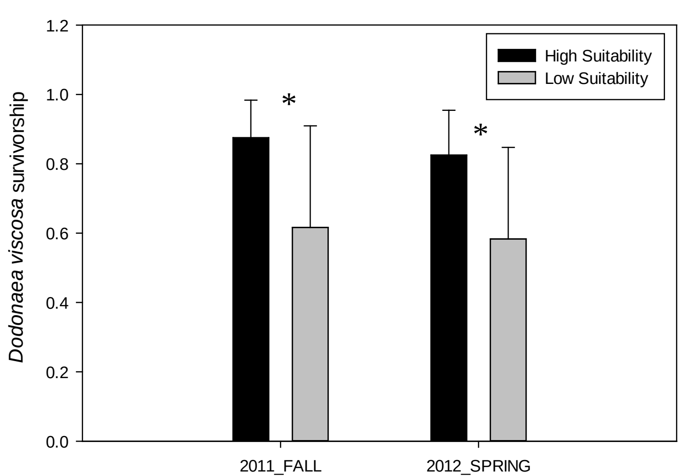

Figure 35. *Survivorship of Dodonaea viscosa outplants among habitat suitability treatments at the shrubland site. Error bars show 1SD. *P<0.05*

Live, Dead, and Total Grass Biomass [Fine fuels]
Live grass biomass (one-way ANOVA, $F_{2, 154} = 4.72$, $p = 0.01$), dead grass biomass (one-way ANOVA, $F_{2, 154} = 18.49$, $p<0.001$), total grass biomass (one-way ANOVA, $F_{2, 154} = 10.58$, $p<0.001$), and live:dead ratio (one-way ANOVA, $F_{2, 154} = 9.98$, $p<0.001$) varied among sites (Fig. 36). The Shrubland had the highest dead biomass and total biomass. KAA had the highest live biomass and live:dead ratio.

At KAA, total biomass, live biomass, and Live:dead ratio ($F_{1, 39} = 5.51$, $p=0.024$) was higher in 2009 and lower in 2010 (Fig. 37a). There were no treatment effects on live:dead, live biomass, or total biomass at KAA.

In the Shrubland, dead ($F_{2, 50} = 23.69$, $p<0.001$) and total biomass ($F_{2, 50} = 21.07$, $p<0.001$) was highest in August 2010 and lowest in January 2010 (Fig. 37b; $F_{2, 50} = 23.69$, $p<0.001$). Live biomass was highest in February 2009 (Fig. 37b). Dead ($F_{1, 50} = 6.59$, $p=0.013$), live ($F_{1, 50} = 7.93$, $p=0.007$), and total ($F_{1, 50} = 7.42$, $p=0.009$) biomass were higher in high suitability habitats, compared to low suitability. Weed control was the only significant factor in models of live:dead ($F_{1, 50} = 8.61$, $p=0.005$). Live:dead was lower in the plots that were weeded.

At PWW, dead biomass ($F_{1, 47} = 6.89$, $p=0.012$) and total biomass ($F_{1, 47} = 7.48$, $p=0.009$) were reduced by weed control but no other factors. No significant effects on live biomass (Fig. 37c). Live:dead was higher in plots that were weeded ($F_{1, 47} = 12.77$, $p=0.001$).

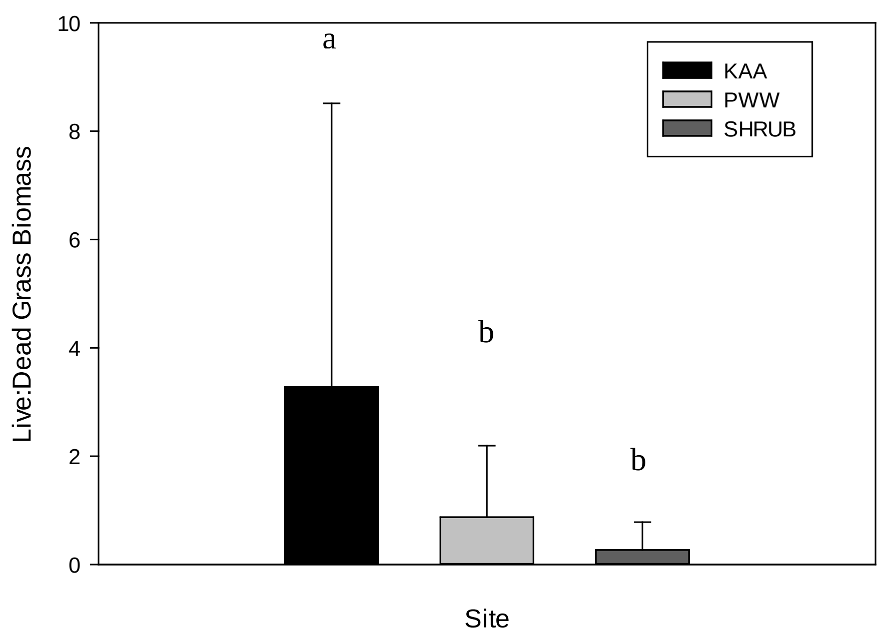

Figure 36. *Live:dead grass biomass of all sites. Error bars show 1SD*

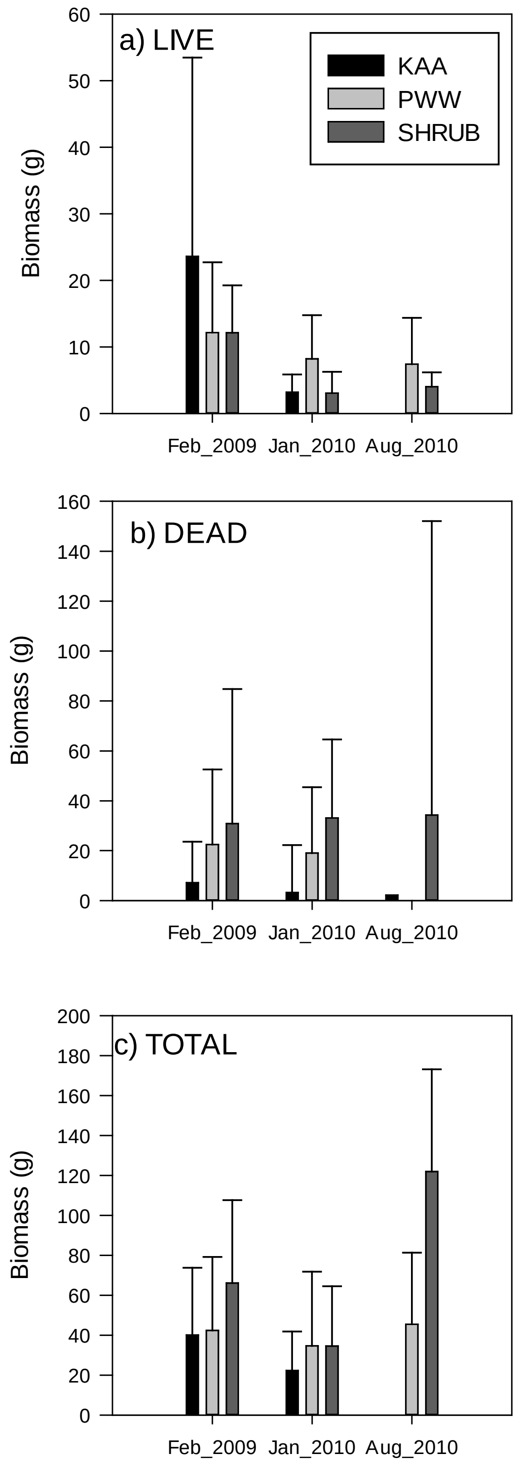

Figure 37. *Live, dead, and total grass biomass by site. Error bars show 1SD. A) LIVE, B) DEAD, C) TOTAL*

Abundance Data

KAA had the highest native cover in the understory, followed by the shrubland (one-way ANOVA, $F_{2,316} = 100.64$, $p<0.001$; Fig. 38). PWW had the lowest native cover. PWW had higher nonnative cover than KAA or the Shrubland (one-way ANOVA, $F_{2,316} = 6.66$, $p=0.001$; Fig. 38).

At KAA, species addition ($F_{2,99} = 4.65$, $p=0.012$; Fig. 39a), habitat suitability ($F_{1,99} = 23.82$, $p<0.001$; Fig. 39b), and species addition x weed control ($F_{2,99} = 4.21$, $p=0.018$; Fig. 39c) affected native cover. Date ($F_{2,99} = 21.30$, $p<0.001$; Fig. 40a), weed control ($F_{1,99} = 54.69$, $p<0.001$; Fig. 40b), and habitat suitability ($F_{1,99} = 7.72$, $p=0.007$; Fig. 40c) affected nonnative cover.

At the Shrubland, Date ($F_{2,99} = 3.67$, $p=0.029$; Fig. 41a), weed control ($F_{1,99} = 5.64$, $p=0.019$; Fig. 41b), and habitat suitability ($F_{1,99} = 14.58$, $p<0.001$; Fig. 41c) affected native cover. Date ($F_{2,99} = 11.21$, $p<0.001$; Fig. 42a), weed control ($F_{1,99} = 253.05$, $p<0.001$; Fig. 42b), species addition ($F_{2,99} = 3.83$, $p=0.025$; Fig. 42c), habitat suitability ($F_{1,99} = 29.37$, $p<0.001$; Fig. 42d), and species addition x weed control ($F_{2,99} = 4.22$, $p=0.017$) affected nonnative cover.

At PWW, Date ($F_{2,94} = 8.29$, $p<0.001$; Fig. 43a), species addition ($F_{2,94} = 12.13$, $p<0.001$; Fig. 43b), and habitat suitability ($F_{1,94} = 8.97$, $p=0.004$; Fig. 43c) affected native cover. Nonnative cover was lower in weed control treatments ($F_{1,94} = 505.95$, $p<0.001$; Fig. 44).

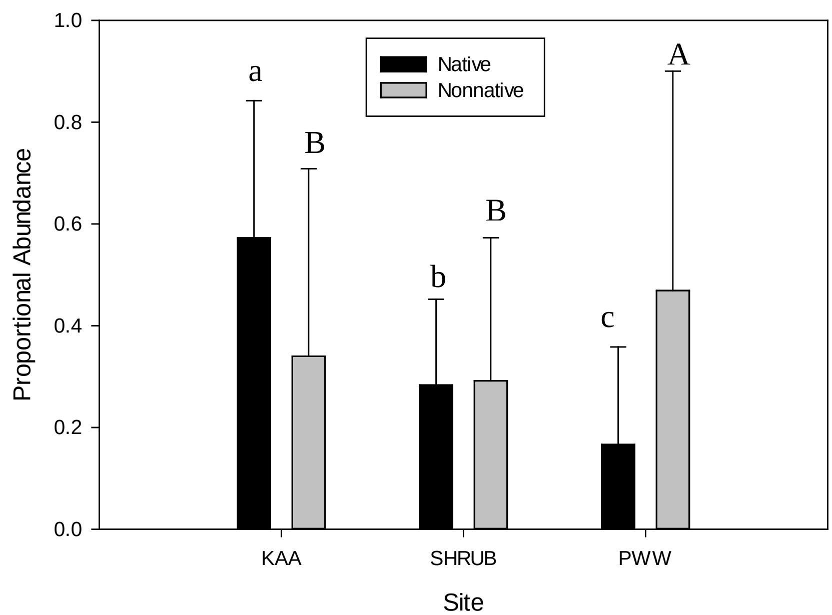

Figure 38. *Native and nonnative species abundance at each site. Error bars show 1SD. Letters indicate statistically different means, Tukey HSD P<0.05. Lower case letters compare native abundance and uppercase letters compare non-native abundance.*

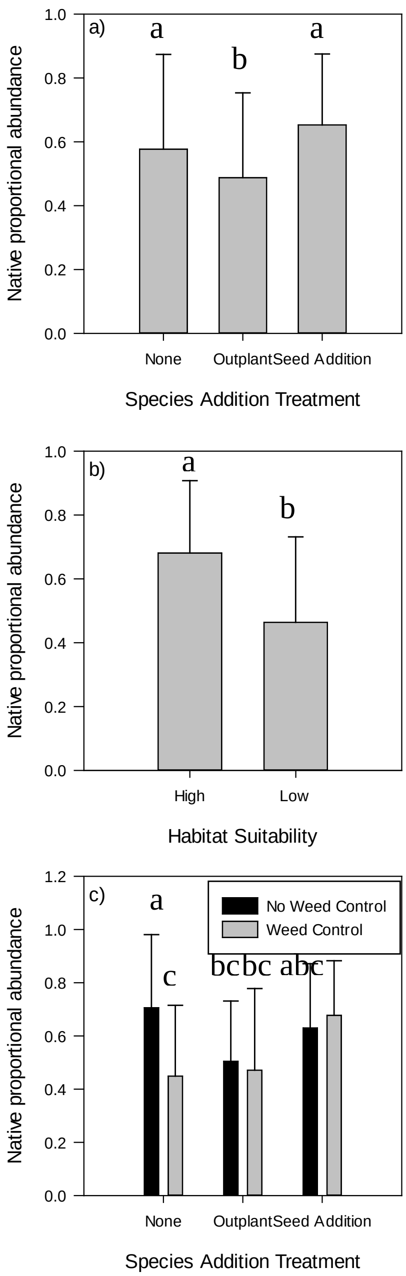

Figure 39. *Native species abundance at Kipuka Alala. Error bars show 1SD. A) as a function of species addition treatment, B) as a function of habitat suitability, C) as a function of species addition and weed control treatments. Letters indicate statistically different means, Tukey HSD P<0.05.*

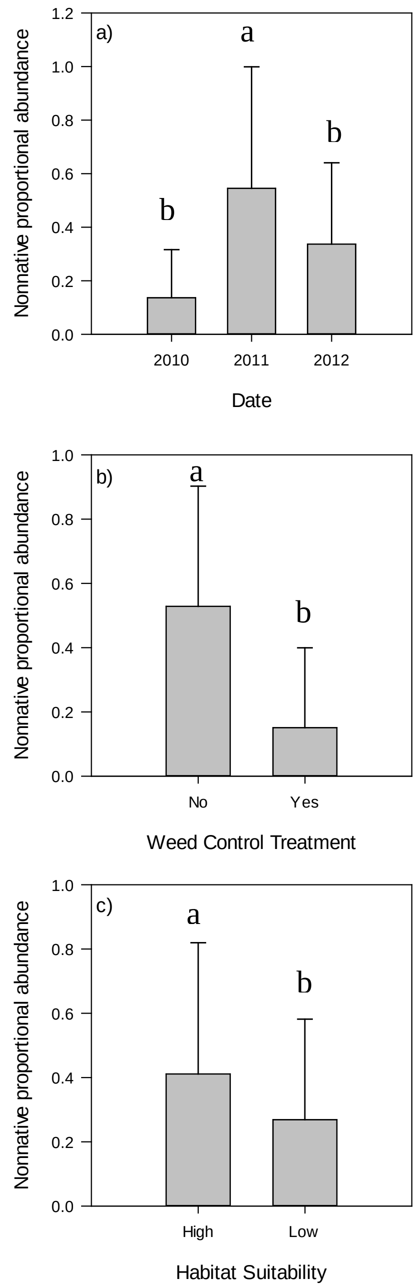

Figure 40. *Nonnative species abundance at Kipuka Alala. Error bars show 1SD. A) as a function of sampling date, B) as a function of weed control treatment, C) as a function of habitat suitability. Letters indicate statistically different means, Tukey HSD P<0.05.*

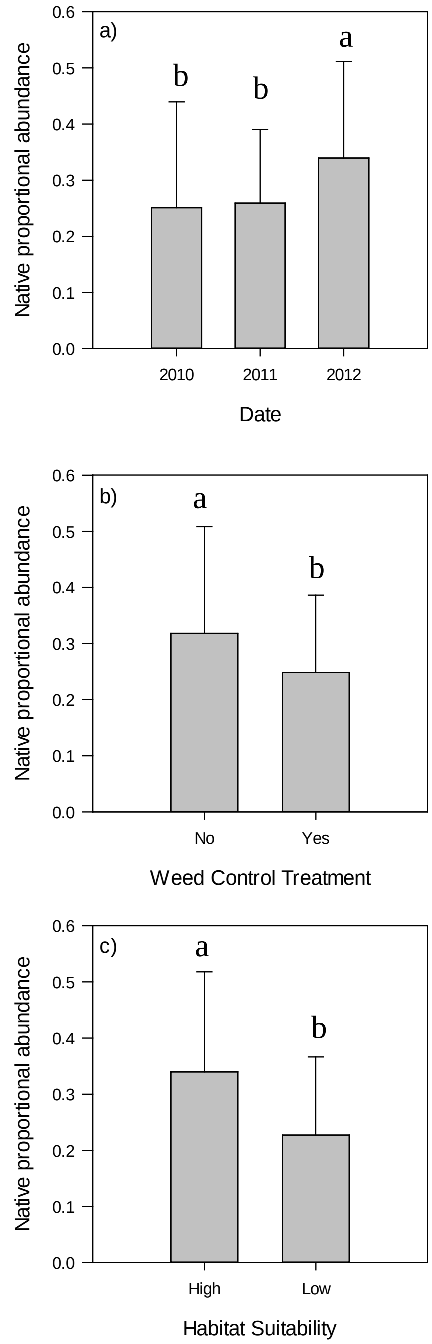

Figure 41. *Native species abundance at the Shrubland. Error bars show 1SD. A) as a function of sampling date, B) as a function of weed control treatment, C) as a function of habitat suitability.*

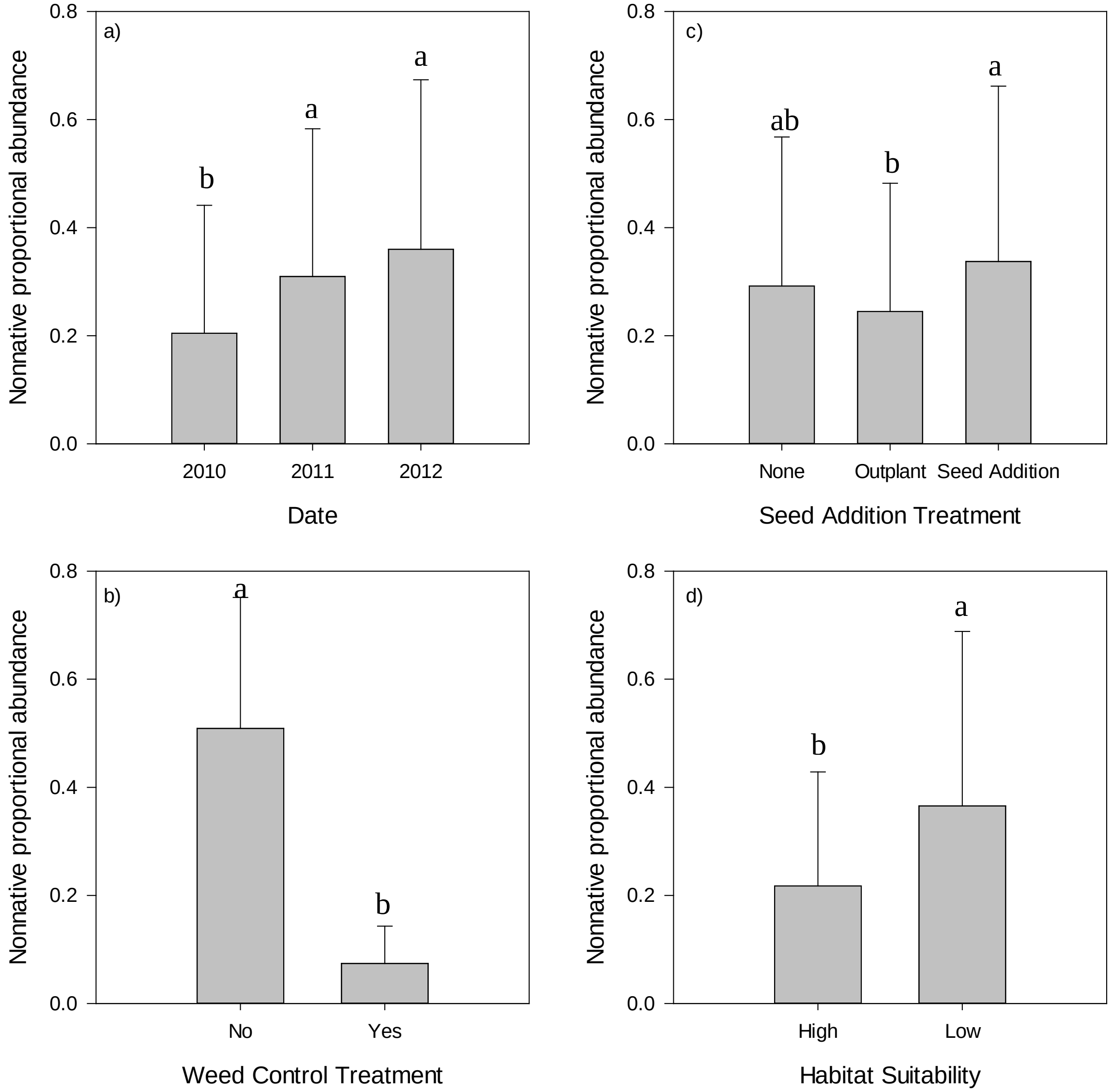

Figure 42. *Nonnative species abundance at the Shrubland. Error bars show 1SD. A) as a function of sampling date, B) as a function of weed control treatment, C) as a function of species addition treatment, D) as a function of habitat suitability. Letters indicate statistically different means, P<0.05.*

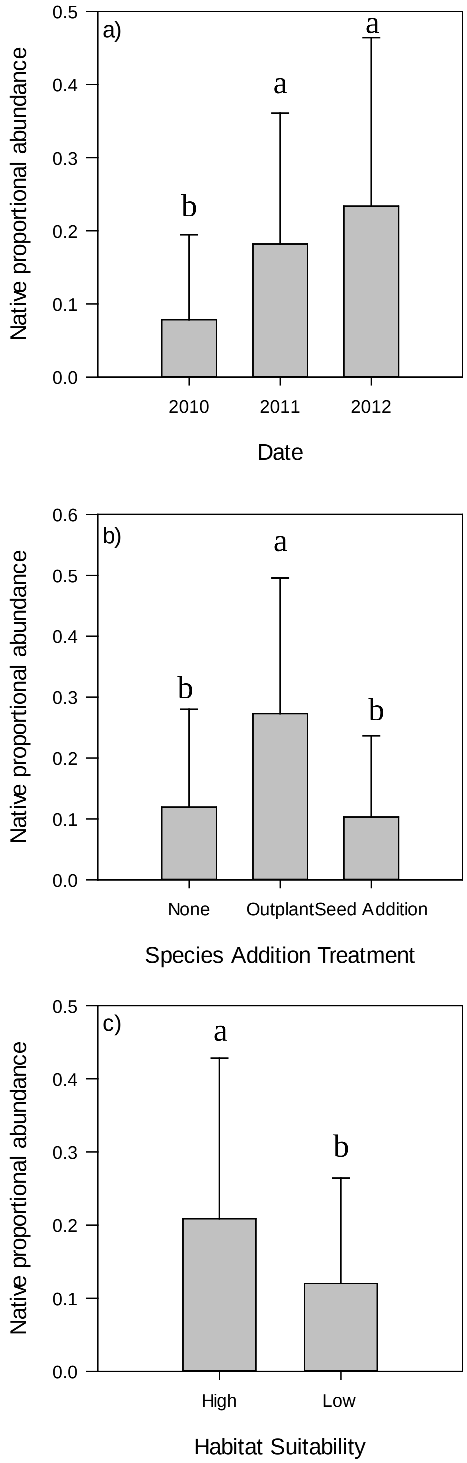

Figure 43. *Native species abundance at Puu Waawaa. Error bars show 1SD. A) as a function of sampling date, B) as a function of species addition treatment, C) as a function of habitat suitability. Letters indicate statistically different means, P<0.05.*

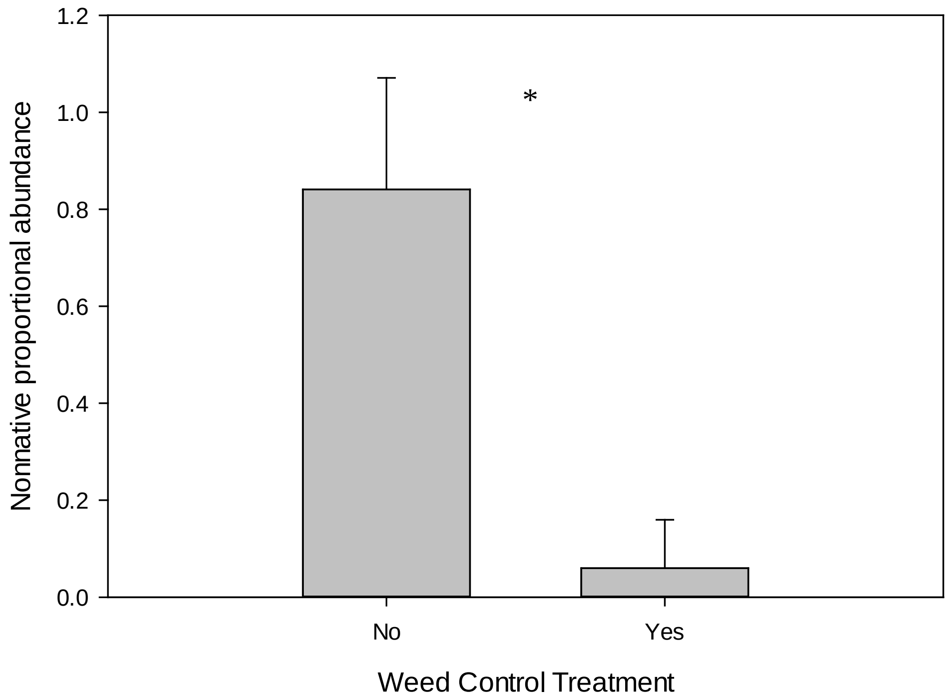

Figure 44. *Nonnative species abundance at Puu Waawaa as a function of weed control treatment. Error bars show 1SD. *P<0.05*

Summary of Restoration Experiments

We hypothesize that difference in treatment effects across sites occur due to differences in rainfall, nutrient availability, and productivity, suggesting that restoration prescriptions should depend on the resource availability and degree of degradation a site experiences. Previous work suggests that active restoration is needed at both high and low levels of resource availability due to high competition with invasive species at high resource levels and low establishment at low resource levels. Whereas, restoration may be more spontaneous at moderate resource levels (Fig. 45, (Prach and Hobbs 2008)). Our sites span a productivity gradient with the high productivity site Puu Waawaa containing high levels of *Pennisetum setaceum* cover, Kipuka Alala occurring at moderate productivity, and the Shrubland and Greenstrip occurring in a low productivity, stressful environment. Thus invasive species control was effective at Puu Waawaa, restoration treatments had reduced effects at Kipuka Alala, and increasing resources through habitat suitability modeling or shade treatments had significant effects at the Shrubland and Greenstrip sites. We expect that similar results would occur across a productivity gradient in other dryland ecosystems; however, this should be studied with future research.

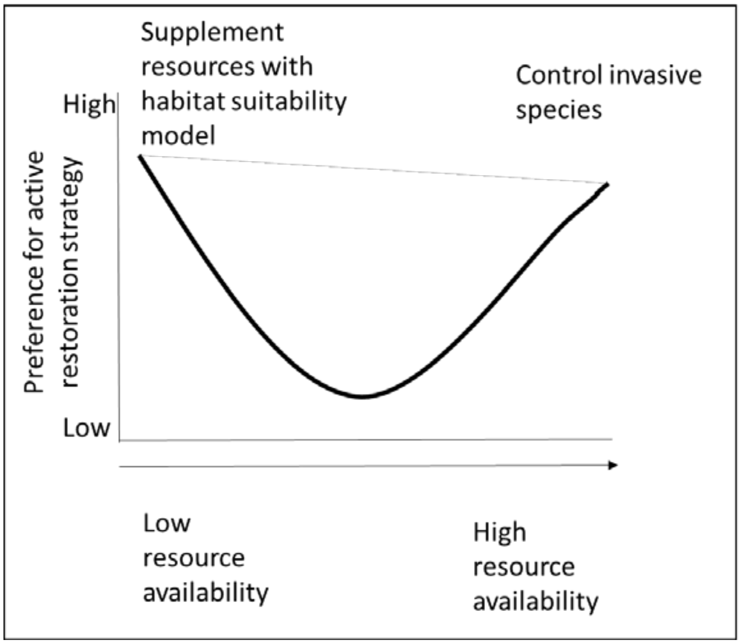

Figure 45. *Preference for an active restoration strategy as a function of resource availability (after Prach and Hobbs 2008).*

Because resources for restoration are limited, we can identify where various restoration activities will have the greatest impact (Table 8). Invasive species removal has the greatest impact at high productivity sites (lowland dry forest). Outplanting is also more successful in these sites, but only when invasive species are removed. Restoration was more difficult in the low productivity sites where environmental conditions were stressful, especially during the drought years of the study. In these areas it may be more effective to remove invasive species (due to their relatively low abundance) and wait for a high rainfall year in which outplanting can occur. Using the habitat suitability model for planting also increases the success of restoration. We also found that active restoration can be a lower priority for moderately invaded, moderate productivity communities which have the capability to maintain a native ecosystem state.

Table 8. Site specific pathways conceptualizing relevance to future management based on restoration metric, treatments applied and initial site conditions. Restoration success is considered as outplant survival or an increase in native cover. Fuel reduction equates to a decrease in fine fuel biomass. A (+) symbol indicates a significantly positive response; a (–) symbol indicates a significant negative response and None indicates no response.

		Initial Productivity	*Low*	*Moderate*	*High*
		Site	*SHRUB*	*KAA*	*PWW*
Metric	**Treatment**				
Restoration success	*Habitat suitability*		**+**	**None**	**None**
	Weed removal		**+**	- **/ None**	**+**
	Outplanting		**None**	**None**	**+**
Fuel reduction	*Habitat suitability*		**-**	**None**	**None**
	Weed removal		**-**	**None**	**+**

4.2.2. Ungulate Impacts

Home ranges for both sexes of feral goats spanned from 3.4 to 60.0 km^2 (Table 9). Male annual home range was 40.0 ± 7.9 km^2 (range 5.9–60.0 km^2) compared to 13.3 ± 4.7 km^2 (range 3.4–27.7 km^2) for females. Similarly, mean annual 50% core use area for males was 8.0 ± 1.9 km^2 (range 1.1–15.1 km^2) compared to 2.9 ± 1.1 km^2 (range 0.8–7.8 km^2) for females. The 95% annual home ranges were significantly larger for males than females (t = 2.65, *d.f.* = 8.67, P = 0.027), but the annual 50% core use areas did not differ statistically between sexes (t = 2.13, *d.f.* = 8.69, P = 0.063). Further, among all feral goats, 5 out of 11 individuals had 7 long-distance movements (Fig. 46). The remaining six individuals demonstrated limited annual variation in home range size and no long distance movement events. Of the five individuals that demonstrated long distance movement, mean movement distance was 7.71 km (SE = 0.63 km).

Table 9. Adaptive-kernel density estimates with *href* for the smoothing parameter of annual home range and core-use area of 13 feral goats in Pohakuloa Training Area on Hawaii Island, 2010–2011.

Goat ID	Monitoring period (#days)	# of points	95% Area (km^2)	50% Core-use Area (km^2)
F1	299	2554	27.7	6.4
F2	363	2519	7	1.3
F3	309	2512	34.7	7.8
F4	363	2990	7.1	1.3
F5	46	381	3.4	0.8
F6	127	636	7.7	1.7
F7	363	2513	5.8	0.9
M1	363	2870	43.3	7.5
M2	363	2568	60	15.1
M3	363	2622	53.8	9.8
M4	363	3033	5.9	1.1
M5	363	2985	44.9	8.5
M6	363	2925	31.9	6.2
Mean male 95% area			**40.0 ± 7.9 km^2**	
Mean female 95% area			**13.3 ± 4.7 km^2**	
Mean male 50% area			**8.0 ± 1.9 km^2**	
Mean female 50% area			**2.9 ± 1.1 km^2**	

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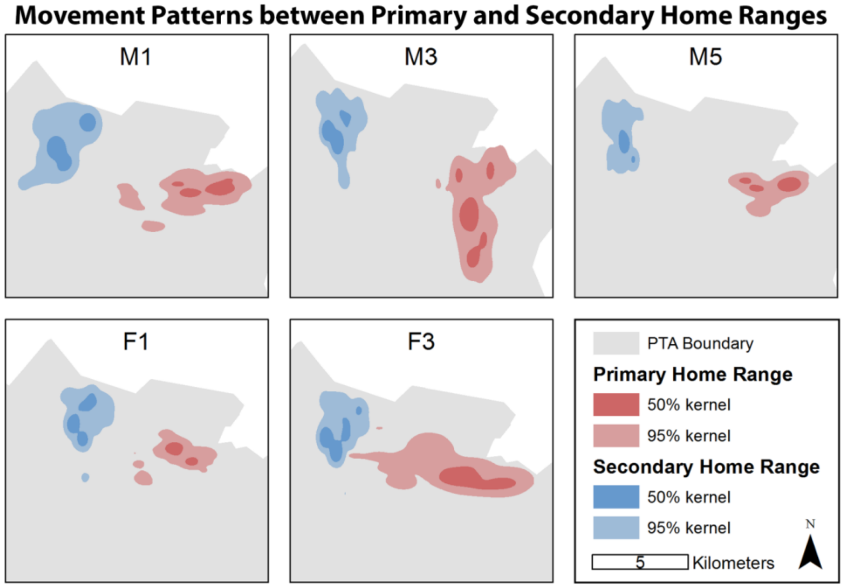


Figure 46. *Primary and secondary home ranges of long-distance movement feral goats. Adaptive kernel home ranges for 5 non-native feral goats that moved between non-overlapping home ranges in Pohakuloa Training Area on Hawaii Island, 2010–2011. Red areas indicate 50% (dark red) and 95% (light red) primary ranges and blue areas indicate 50% (dark blue) and 95% (light blue) primary ranges. All individuals moved WNW to the only region of the study area that experienced significant vegetation green-up.*

Our estimates for the sizes of home ranges for feral goats in Hawaii are within the range of estimates (0.4–246.5 km^2) for other dryland habitats (O'Brien 1984, King 1992). In comparison to these other studies, home ranges in our study encompassed a similar amount of space, but 50% core use areas were substantially smaller than annual ranges. This difference suggests that feral goats used space non-randomly, returning to multiple core use areas within annual ranges. Based on collar data and field observations, core areas were bedding grounds used on a nightly basis. These bedding grounds often included areas of high topographic variability with high lookout points, a valuable resource for predator detection and avoidance (Coblentz 1978).

Mean NDVI values in primary and secondary home ranges showed similar trends over one year. Both primary and secondary ranges showed an increase in NDVI during the second half of the study associated with increases in the frequency and intensity of precipitation events (Fig.47). However, a greater increase in NDVI occurred in secondary vs. primary home ranges of all dispersing individuals. Specifically, four out of five individuals dispersed to a secondary range that had significantly higher NDVI values compared to their primary ranges (Table 10). Based on NDVI values of primary and secondary home ranges of dispersing individuals calculated with kernel density estimators, results support the hypothesis that feral goats travelled to areas of recent vegetation green-up following pulse precipitation events. Some limitations existed in our study; in particular, how human activity on this active military base may influence feral goat movement. However, the patterns that we observed suggest that the NDVI is a good indicator of habitat and movement patterns of feral goats in tropical island dry landscapes.

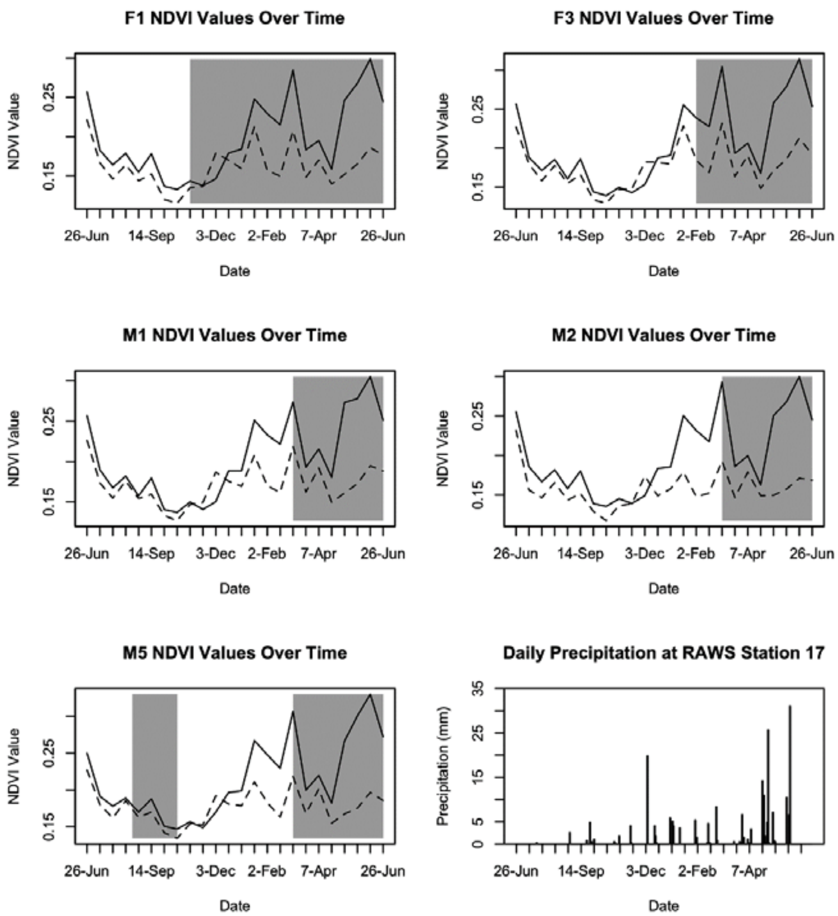


Figure 47. *Phenology of feral goat movement. A comparison of mean Normalized Difference Vegetation Index (NDVI) values in primary and secondary ranges of non-native feral goats in Pohakuloa Training Area on Hawaii Island, 2010–2011. White regions of the graph represent time when individuals are located in Primary Ranges and shaded regions represent time when individuals are located in Secondary Ranges. The mean NDVI value of individual Primary and Secondary ranges are represented by dotted and solid lines, respectively.*

Table 10. One-tailed probabilities for differences in relative NDVI values between primary and secondary ranges of feral goats in Pohakuloa Training Area on Hawaii Island, 2010–2011.

Goat ID	*z-score*	V	*p*	Higher NDVI range
F1	-0.14	17	0.945	n.s.
F3	-2.7011	1	0.008	Secondary
M1	-2.5205	0	0.016	Secondary
M2	-2.2404	2	0.046	Secondary
M5	-2.4006	6	0.028	Secondary

doi:10.1371/journal.pone.0119231.t002

Both males and females demonstrated long-distance movement, and each movement was unidirectional. With the exception of two individuals, feral goats dispersed at different times throughout the year. Each movement was a shift from the eastern section (primary range) to northwestern section (secondary range) of PTA, and each long-distance movement was consistent with the hypothesis that feral goats respond to intra-seasonal vegetation dynamics on

small temporal scales by traveling to areas of recent vegetation green-up. Mean secondary home range size was slightly smaller than mean primary home range size, suggesting that increased resource availability associated with vegetation green-up requires less space-use by feral goats. While the difference in area between primary and secondary home ranges had no statistically significant difference, there may be an ecologically significant difference undetected due to small sample size. Feral goats may have avoided areas of human disturbance including structures, a gravel pit mine, and intermittent high-volume vehicular traffic. In addition, large fenced exclosures prevented the movement of animals into certain areas, which were incorporated into spatial analyses by masking these fenced areas during home range estimation. However, military training and other human activities were not available for assessment as a temporal factor influencing animal movement.

Based on our findings, strong evidence exists that feral goats move to areas of high NDVI values following pulse precipitation events in dry montane landscapes on tropical islands. Movement patterns of collared feral goats in PTA suggest neither nomadic behavior nor migration. Further research over a longer observational period (>1 year) would help determine if the movement patterns observed in this study are the result of ultimate or proximate causation. Results presented here contribute to a growing field of research in movement ecology that combines GPS telemetry data with remotely sensed phenological data to test hypotheses of herbivore movement in response to pulses in primary productivity. Although seasonality in the tropics is not as pronounced as temperate regions, PTA is a dry system that is characterized by both low and variable precipitation. These conditions occur in dry ecosystems throughout the world and offer important implications for conservation and management beyond just Pacific Islands.

4.2.3. Experimental Tests of Post Burn Restoration and Invasion through Enemy Release

There are numerous mechanisms that can explain invasions including: anthropogenic disturbance, enemy release, asymmetry in effective dispersal supply, etc. These mechanisms rely on an assumption that native species could outcompete invaders if a "natural" state existed (e.g., no disturbance, no alteration in enemies, etc.). Superior competitive ability of invasive species is another mechanism to explain invasive success. In Hawaii and other isolated islands, it is easy for invaders to be superior competitors because the floras are depauperate and disharmonic, and native plant communities may not compete well with invasive colonists (Reaser et al. 2007). Thus, in Hawaii invasion may result from anthropogenic disturbance, reduced effective dispersal supply, a lack of defense to herbivores, and a lack of competition from its disharmonic flora (Denslow 2003).

Figure 48. *Senecio madagascariensis.*

Our recent work funded through this SERDP project (see Kellner et al. 2011 for details) suggests that anthropogenic disturbance (i.e., the introduction of ungulates) facilitated the invasion of *Senecio madagascariensis* (fireweed, Fig. 48) into

Mamane-Naio communities within Pohakuloa Training Area (PTA) through a special case of enemy release. The removal of non-native herbivores had a positive effect on *Senecio* and no effect on native plant species, suggesting that herbivore removal may contribute to *Senecio* invasion. Native plant populations may have no response to ungulate removal because they continue to be regulated by their specialist herbivores, whereas *Senecio* does not have specialist herbivores in Hawaii.

We proposed a study to test an alternative hypothesis, that removal of ungulates has the potential to increase native population growth as well, but native populations have been decimated by disturbance and there is an insufficient native species pool to take advantage of the removal (asymmetry in effective dispersal supply between natives and invasives). We tested the relative contribution of ungulates, effective dispersal supply, and competitive interactions on *Senecio* invasion and addressed the following questions: Is *Senecio* competing with natives or not? How do ungulates change the rules for this competition? Can native species pools be altered to overcome an asymmetry in effective dispersal supply? This is a critical time for this research since we are on the "front" of this invasion and we have found evidence that *Senecio* can contribute significantly to vegetation fuel loading, increasing fire risk in these ecosystems. We manipulated the presence of ungulates, native species effective dispersal supply, and competitive interactions between native and invasive species to better understand what controls invasion and how to better manage this invasion front. We chose to replicate the experiment in one Mamane-Naio forest that recently burned and one that is unburned in order to examine the effect of fire on *Senecio* invasion and native-invasive plant interactions. Performing the experiment in a recent burn also allowed us to remove all existing biomass thereby equalizing opportunities for native and invasive species. It also creates a lot of bare ground, a condition that is similar to heavy ungulate use (e.g., in Kipuka Alala before removal), and test which restoration prescriptions increase native diversity and reduce invasion following a fire.

Overall we found that seed availability had the greatest impact on the recruitment of native species and *Senecio*. The presence of herbivores had a negative effect on the recruitment of native species. The presence of herbivores had a positive effect on *Senecio* recruitment, and a negative effect on *Senecio* biomass. Herbivores may reduce the size of *Senecio* plants, but increase the number of individuals. Herbivores may contribute to "invasional meltdown", in which they facilitate *Senecio* invasion by reducing interspecific competition with native populations while also reducing intraspecific competition.

Fire

Recruitment and plant biomass were very low on the unburned site and significantly increased on the Burned site (Table 11). This increase may be the result of a pulse of increased nitrogen (N) that was made available following the fire; however, significant erosion of the surface soil occurred following the fire. This may account for the extreme loss of available phosphorus (P) in this system (Fig. 49). Bray and Kurtz-1 soil P (PO_4) mean values were two times higher in burned MSDF than unburned MSDF sites and 10 times greater than DVS (areas of high and low suitability measurements). ANOVA on PO_4 values yielded significant variation among MSDF and DVS conditions ($F_{2,26}$= 57.08, P < 0.001). Post-hoc comparisons using Tukey's HSD test indicate that the mean value in burned MSDF (100.2 mg/kg, SE = 12.3) was significantly different from unburned MSDF (227.3 mg/kg, SE = 20.3) and DVS (18.55 mg/kg, SE = 3.91). In

short-stature DVS on the 65 ky substrate, where a pervasive prehistoric fires history exists, available PO_4 was an order of magnitude less than in unburned MSDF. Redfield ratios of foliar nutrients in DVS and MSDF suggest that P is limiting in DVS, but not in unburned MDSF. Additional measurements of available P in areas with known fire histories will be necessary to determine whether Pleistocene-aged substrates in our study are P-limited, and the underlying causes of P limitation. With no roots to hold the soil in place, we witnessed the high winds in this region blowing large amounts of soil. These strong winds made it difficult to quickly suppress this fire and could contribute to the removal of organic matter and nutrients over a longer time period. Therefore, the plant response to the initial pulse of N may be temporary and the chronic loss of topsoil could have longer-term impacts on the development of the plant community.

Table 11. Comparisons between burned and unburned site. Test statistics and P-values are reported for Kruskal-Wallis tests used to analyze data from the final census in July 2011. Mean ± SE are calculated over all experimental plots in each site (N = 40 per site for seedling recruitment and abundance data; N = 10 per site for soil nitrogen data). Units for soil nitrogen are ug analyte per g dry soil.

Response Variable	**Burned Site Mean**	**Unburned Site Mean**	**H**	**P**
Seedling recruitment (# seedlings/plot)				
Senecio	1.300 (0.353)	0.275 (0.160)	10.74	**0.001**
Native	0.425 (0.160)	0.050 (0.035)	5.37	**0.021**
Abundance (% cover)				
Senecio	5.70 (1.59)	0.40 (0.28)	11.49	**0.001**
Total Native	0.40 (0.24)	0.40 (0.31)	0.19	0.663
Total Non-native	28.20 (3.97)	27.00 (2.85)	0.10	0.746
Total Vegetative	28.90 (3.95)	28.70 (3.16)	0.21	0.650
Biomass (g)				
Senecio	30.57 (9.31)	0.44 (0.19)	7.42	**0.006**
Native	22.5 (15.6)	0.015 (0.01)	4.09	**0.043**
Soil nutrients				
Total Available N	64.6 (24.1)	13.42 (2.63)	3.86	**0.049**
NH_4	51.7 (23.9)	4.21 (0.82)	4.17	**0.041**
$NO_2 + NO_3$	12.92 (4.16)	9.22 (1.94)	0.14	0.705

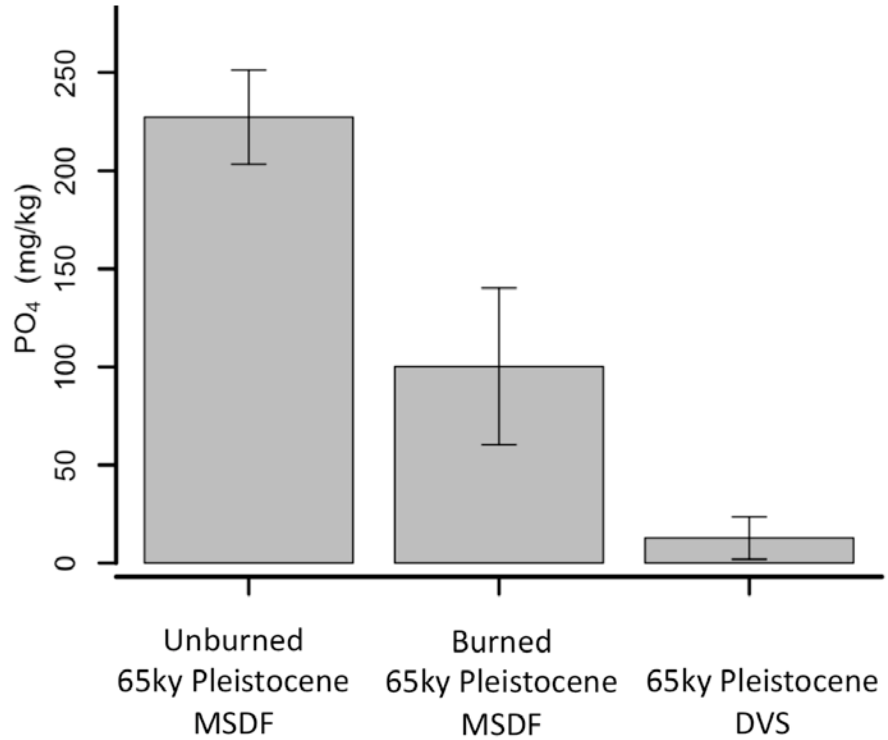


Figure 49. *Plant available phosphorus measured in 65 ky Pleistocene aged substrates on MSDF dry forest areas after a 2010 wildfire event and 65 ky Pleistocene aged substrates on DVS shrubland areas*

Dispersal limitation

Overall we found that seed availability had the greatest impact on the recruitment of *Senecio* and the native species studied. The seed addition treatments significantly increased seedling recruitment, cover, and biomass of all species (Table 12; Figs. 50, 51). We expected that native species would be dispersal-limited in this region, but were surprised that *Senecio* was also strongly dispersal-limited. Native plant populations are small as a result of prior disturbance and browsing by invasive ungulates. In addition, many of the species we used in our experiment have relatively large seeds that likely do not disperse long distances. An exception is *Chenopodium oahuense*, which produces many small seeds that occurred in high numbers at our sites (Fig. 52). *Senecio* is a wind-dispersed species, typical of other species in the Asteraceae. Because it occurs in high abundance at sites nearby we expected *Senecio* to occur naturally in the seed rain and were surprised that its seed numbers were very low (Fig. 52). The areas used for this experiment occur in a large valley between the Mauna Loa and Mauna Kea volcanoes, where winds are not impeded by landforms and wind speeds are high (Interpolated, 30-m wind speeds for our sites range from 22 to 25 kmph; Wind Energy Resource Data map). These high winds may limit the ability of *Senecio* seeds to become established, and instead seeds are blown to other areas where they are deposited.

Table 12. Experimental treatment effects in the burned site. Test statistics (F) are reported for general linear models that included the following factors: Block DF = 8; Fence DF = 1; Senecio Seed DF = 1; Native Seed DF = 1; Interaction Terms DF = 1; Error DF = 25. We used a square-root transformation for *Senecio* cover and a reciprocal transformation for *Senecio* and Native biomass. Native cover was too low to analyze. Analyzed data are from the final census of the experiment in July 2011. Significance level: *** ≤ 0.001; **< 0.01; * <0.05, $^{+}$ ≤ 0.07

Response Variable	Block	Fence	Senecio Seed	Native Seed	Fence x Senecio Seed	Fence x Native Seed	Senecio Seed x Native Seed	R^2
Senecio								
Seedling density	2.19^{+}	2.06	25.90***	2.20	6.47*	2.20	3.64^{+}	71.40
Cover	0.88	1.90	16.70***	0.41	0.15	3.92^{+}	0.07	54.49
Biomass	0.49	0.30	28.53***	0.18	1.46	4.84*	1.37	61.82
Native species								
Seedling density	1.17	2.03	0.03	3.53^{+}	2.36	3.53^{+}	0.26	46.13
Biomass	1.54	0.74	0.30	3.61^{+}	1.52	0.85	0.48	39.32

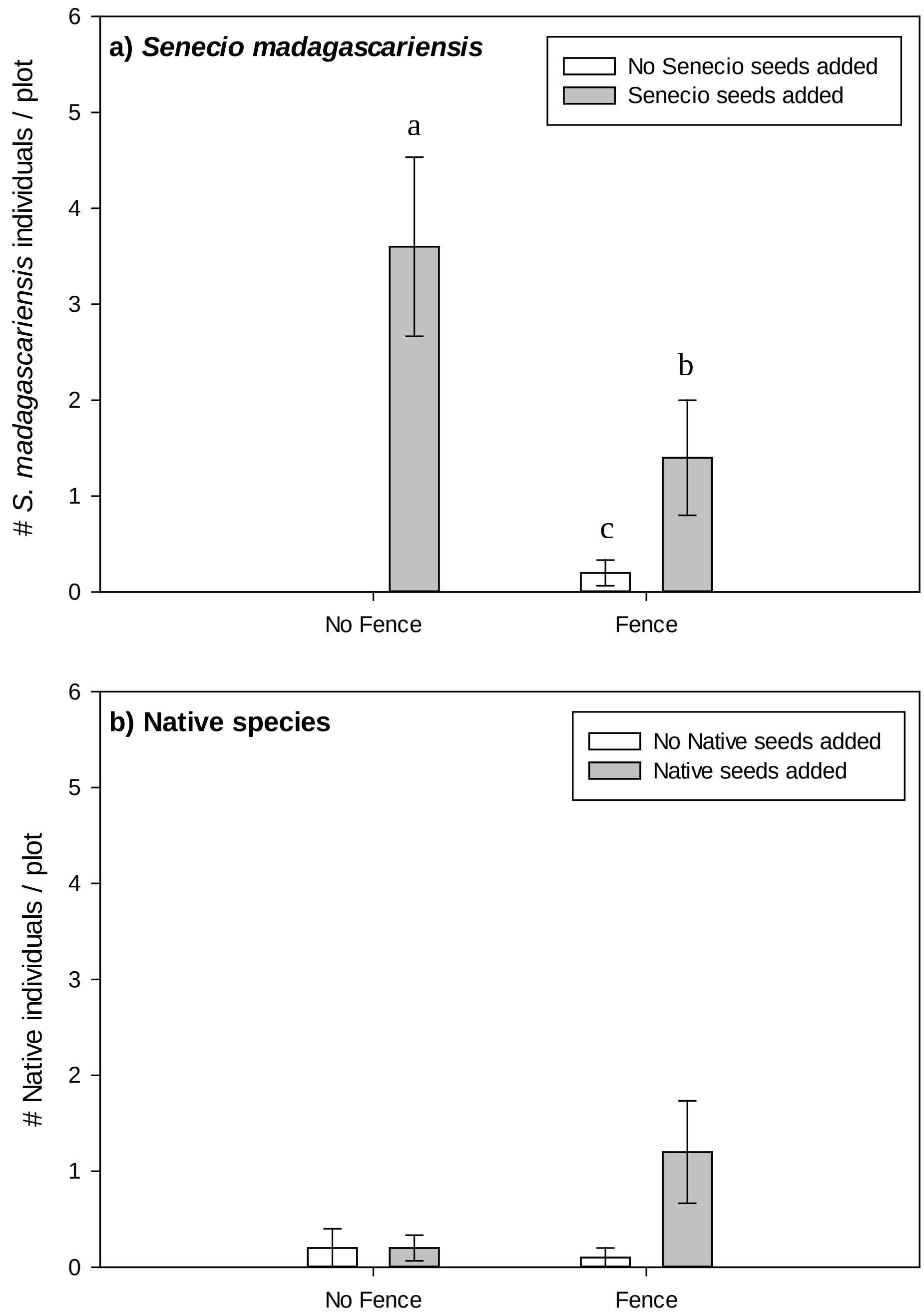
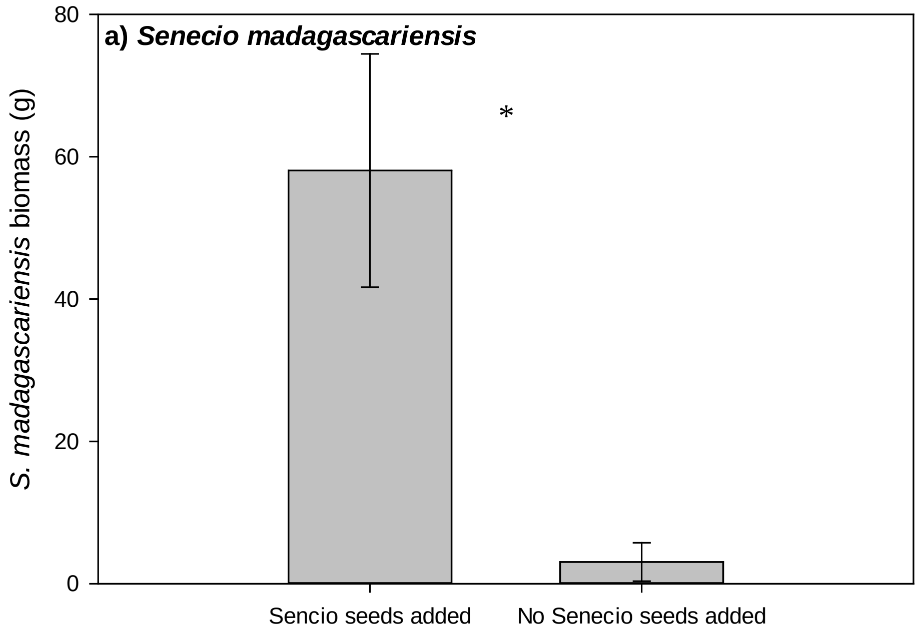


Figure 50. *Recruitment as a function of seed addition and herbivore removal. Bars show mean number of individuals for seed addition (+/-) treatments crossed with herbivore removal treatments (fence/no fence) for a) Senecio madagascariensis and b) all native species combined. Error bars show one SE. Recruitment of Senecio was greatest when Senecio seeds were added and herbivores were present. Native recruitment was greatest when native seeds were added and herbivores were excluded. Letters indicate statistically different means, P<0.05*



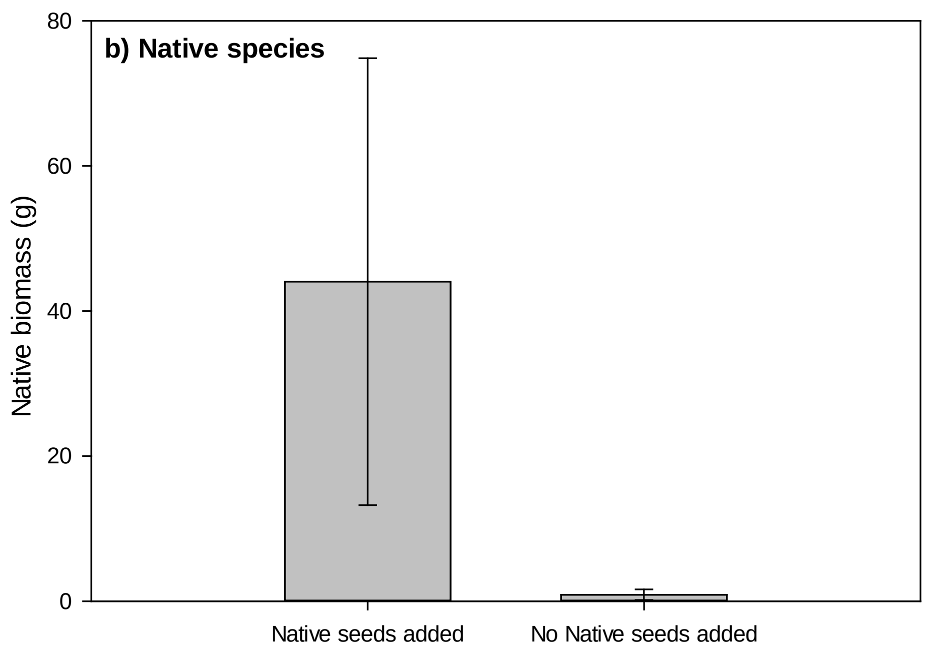


Figure 51. *Seed limitation of biomass. Bars show mean biomass (g) for treatments with and without seed added for a) Senecio madagascariensis and b) all native species combined. Error bars show one SE. Biomass of Senecio and native species increased when seeds were added. *P < 0.05*

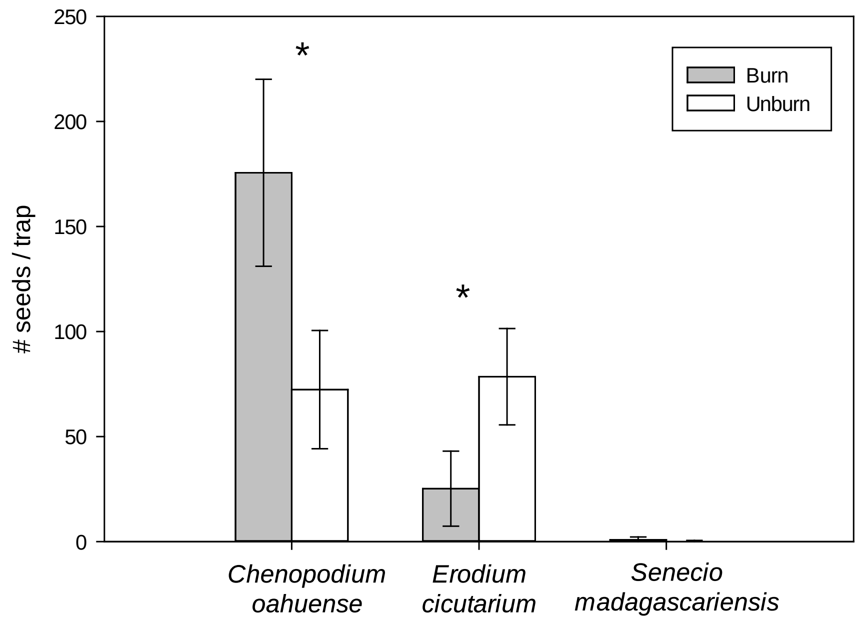


Figure 52. *Seed rain at each site. Data are shown for Senecio madagascariensis and the two most abundant species, Chenopodium oahuense, a native shrub, and Erodium cicutarium, a non-native invasive forb. More Chenopodium seeds were collected from the burned site; More Erodium seeds were collected from the unburned site. Few Senecio seeds were collected at either site. Error bars show one SE. *Kruskal-Wallis test between sites, P < 0.05*

Resources and plant-animal interactions
We replicated our study in a burned and unburned area in order to examine how resources and disturbance may change the relationship between invasive ungulates and invasive plant species; however, our study also coincided with period of extreme drought in the region. The overall low recruitment at both sites suggests that drought likely had a strong, limiting effect on plant population dynamics. Even while watering all plots during the experiment, volumetric soil water content remained low and did not exceed 0.16 m^3/m^3 during the time of the study (Questad et al., unpublished data). Plants were likely water-limited and could not fully take advantage of any soil nutrient or other resource pulses following the fire. In addition there were no main effects of our fencing treatments on any response variables. Therefore, it is still difficult to isolate the role of resources and ungulates in *Senecio* invasion, but several results suggested that invasional meltdown may be occurring, and not enemy release. A bigger question and perhaps more interesting interpretation of these results relates to the impact of severe droughts on the dynamics and regulation between native and invasive species.

Under the Enemy Release Hypothesis (ERH), we expected the following: (1) *Senecio* will have lower abundance when herbivores are present; (2) *Senecio* will have a competitive advantage over native species when herbivores are removed; (3) Native species will benefit most from treatments without *Senecio* that are also protected from herbivores. We found that (1) *Senecio* had higher recruitment, but lower growth, when herbivores were removed; (2) Recruitment and biomass of *Senecio* and native species was similar when herbivores were removed (Figs. 50, 51); (3) Native species benefitted from herbivore removal, but there was no additional benefit in

removing *Senecio* (i.e., no evidence of interspecific competition). Therefore, we did not find strong support for the ERH.

The presence of invasive generalist herbivores had a negative effect on the recruitment of native species (Fence x Senecio interaction, Table 11, Fig. 50b), as expected under both ERH and invasional meltdown. Interestingly, the presence of herbivores had a positive effect on *Senecio* recruitment whether or not native species were also present. This result could occur because *Senecio* is adapted to ungulate browsing in its native range. The presence of browsing ungulates induces the production of pyrrolizidine alkaloids in *Senecio*, making it more resistant to herbivory in general (Joshi and Vrieling 2005). Therefore, this result seems more consistent with the invasional meltdown hypothesis, in which ungulates negatively affect native species while facilitating *Senecio's* tolerance to herbivory.

Wind

Although we did not explicitly test the effects of wind on invasion, results of this and other ongoing studies suggest that wind may play an important role in invasion dynamics in this ecosystem. Wind has significant effects on the behavior and spread of fires across a landscape (Beer 1991, Fendell and Wolff 2001). The high winds in our study region make wildfires difficult to suppress, and lead to large fire extents. Wind accelerates erosion and can lead to nutrient loss, especially following a fire when high levels of erosion occur. The combination of high winds with the volcanic ash substrate in our study system accelerates erosion and may lead to a depletion of topsoil, organic matter, and beneficial microorganisms from the ecosystem. Feral goats in this ecosystem spend a greater amount of time in areas protected from the prevailing winds (M. Chynoweth and E. Questad, *unpublished data*). These areas also have the most suitable microclimates for plant growth due to reduced water stress (Questad et al. 2014). We also recorded a surprisingly low number of *Senecio* seeds, suggesting that wind patterns in this region may blow seeds to other areas. Thus, wind, and its interaction with landforms, fire, nutrients, ungulate behavior, and dispersal dynamics, may be a dominant force controlling plant community interactions and invasion in this ecosystem (Swanson FJ et al. 1988).

Conclusion

In summary, we found complex interactions between herbivores and *Senecio* and native plant species; however, we did not find evidence to strongly support the ERH as the main explanation for *Senecio* invasion. Instead, we found evidence for invasional meltdown, whereby invasive ungulates reduce native populations and may also reduce intraspecific competition and increase the number of individuals in *Senecio* populations. We also found that native species and *Senecio* were dispersal limited in this ecosystem. Like other studies, we find that abiotic and biotic properties of the ecosystem may greatly control the spread of *Senecio* into new areas (Levine et al. 2004). In particular, wind and seed availability may influence where *Senecio* is likely to become established.

4.2.4. Greenstrip Experiment

The purpose of the greenstrip study was to identify species for restoration that will reduce the incidence of fire in dryland ecosystems. Ideally a greenstrip would be situated near high value conservation units to act as a buffer between degraded and high quality areas. Due to the time

constraints of a 5 year proposal and space availability on a DoD landscape our ability to build a "true" greenstrip using native plants needed to be simplified to a greenstrip simulation conducted in an isolated area and using shade cloth as a proxy for creating a canopy –like micro-climate. As a result our ability to fully represent the impact of an actual greenstrip may be limited. We used two approaches: 1) a study of fire-related functional traits of the dominant native and invasive plant species, and 2) an experiment to test how restoration treatments can reduce the abundance of *Pennisetum setaceum*, the main source of fine fuels in this ecosystem.

Fuel traits of dominant species

Traits measured relate to ignition probability (fuel moisture content, dead fuel distribution, leaf surface:volume ratio), total heat release (heating value measured by bomb calorimetry), rate of heat release (dead fuel distribution), and rate of spread (fuel moisture content, leaf surface:volume ratio).

Moisture content

Fuel moisture content was measured repeatedly for six native and two nonnative, invasive species. Moisture content was measured on live leaves of all species, dead leaves of herbaceous species, and stems of woody shrubs. Live leaf moisture content varied among sampling dates ($F_{21,1581} = 117.34$, $p<0.001$) and species ($F_{7,1581} = 614.97$, $p<0.001$). A significant date x species interaction occurred because the differences among species were greater during wetter sampling periods ($F_{147,1581} = 17.11$, $p<0.001$; Fig. 53). Dead leaf moisture content varied among sampling dates ($F_{21,589} = 18.08$, $p<0.001$) and species ($F_{2,589} = 18.08$, $p<0.001$). A significant date x species interaction occurred because the differences among species were greater during wetter sampling periods ($F_{42,589} = 6.58$, $p<0.001$). In particular, dead leaves of *Senecio* had higher moisture than the two grass species. Stem moisture content varied among sampling dates ($F_{22,1029} = 25.86$, $p<0.001$) and species ($F_{4,1029} = 260.12$, $p<0.001$). A significant date x species interaction occurred because the differences among species were greater during some sampling periods ($F_{88,1029} = 6.02$, $p<0.001$).

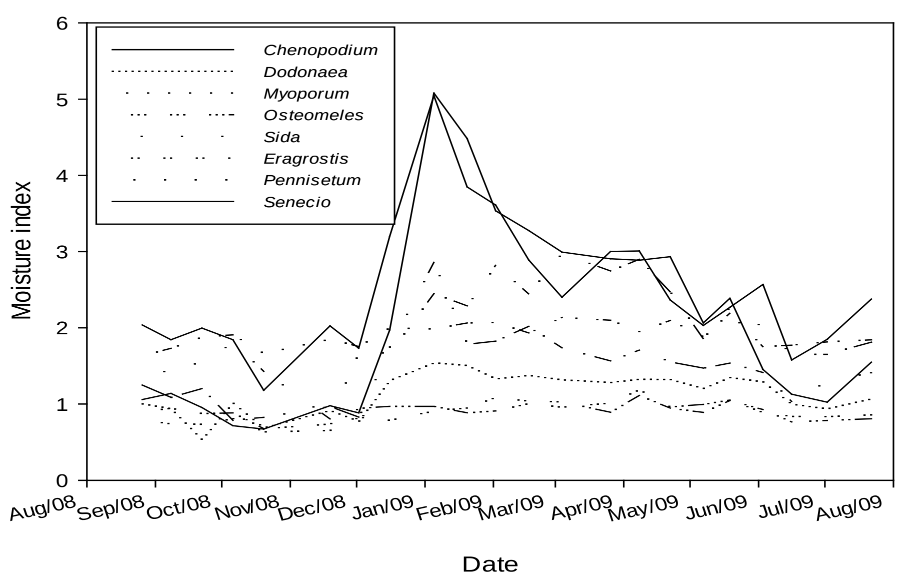


Figure 53. *Leaf moisture index measured as (wet mass – dry mass)/dry mass.*

Distribution of dead biomass

The proportion of dead biomass, measured from percent cover estimates, varied among species ($F_{5,338} = 33.03$, $p<0.001$) but not by sampling date (Fig. 54). *Senecio* had the highest percentage of dead biomass and *Sida* and *Osteomeles* had the lowest.

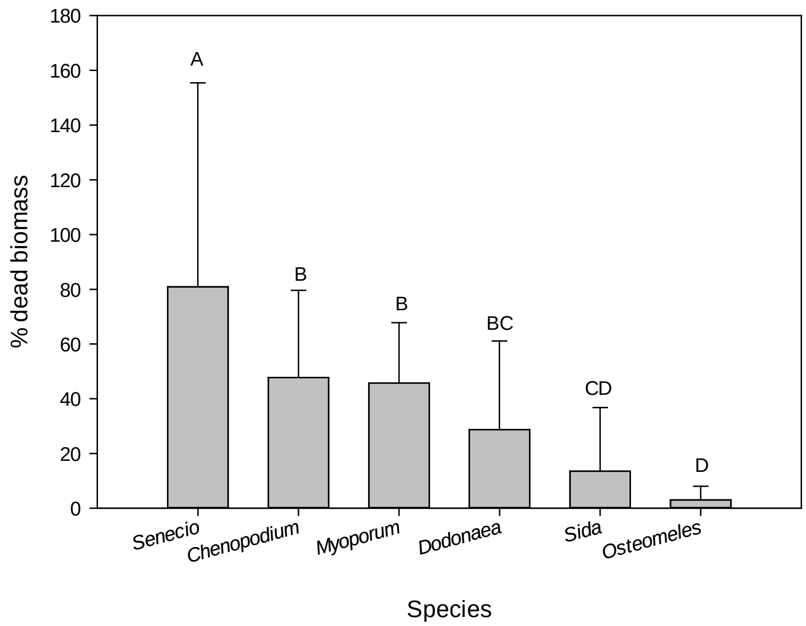


Figure 54. *Percentage of dead biomass.*

Leaf surface:volume

Leaf surface:volume varied among species ($F_{7,464} = 68.41$, $p<0.001$) but not by sampling date (Fig. 55). *Eragrostis* had the highest surface:volume followed by *Pennisetum* indicating that the grasses contribute more to ignition and fuel spread than other species.

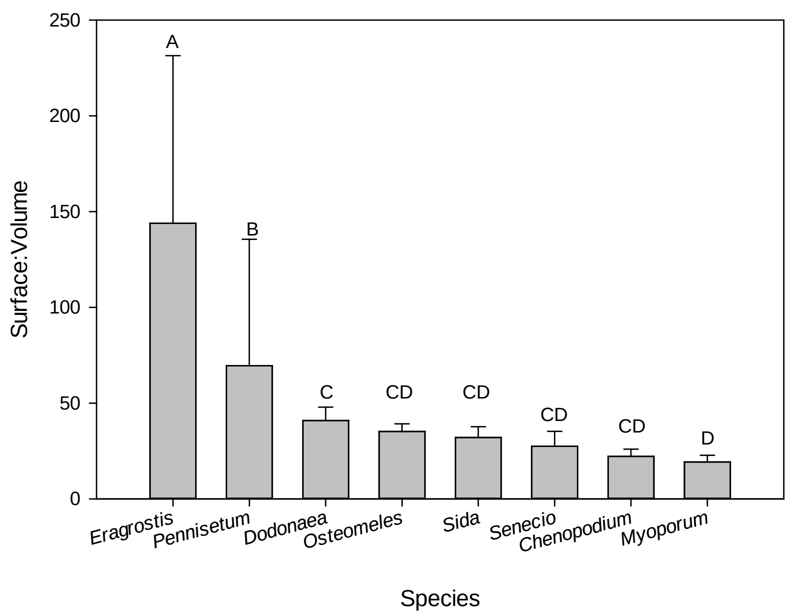


Figure 55. *Surface:volume of leaves.*

Heating value
Heating value varied among species ($F_{7,16} = 13.38$, $p<0.001$) but not by sampling date (Fig. 56). The magnitude of the differences among species was small (Fig. 56).

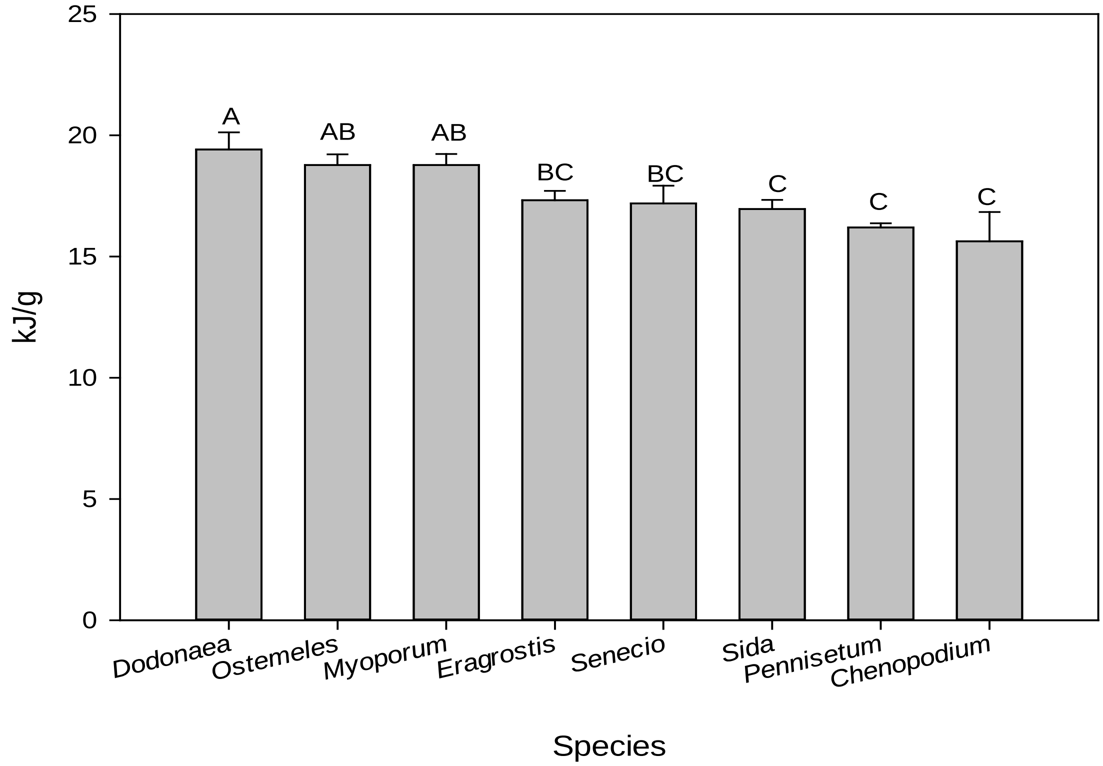


Figure 56. *Heating value of leaves. Mean (SD) of three individuals per species.*

Re-invasion of Pennisetum setaceum
When examining reinvasion into open (unshaded) plots, there were significant differences in reinvasion rates among species treatments ($F_{5,75} = 37.63$, $p<0.001$; Fig. 57). Control treatments with no plants had the highest rates of invasion. All native species plots significant reduced invasion compared to the controls. Plots containing *Eragrostis* had intermediate levels of invasion, whereas plots containing *Chenopodium* had the lowest levels of invasion. These results are in contrast to the limiting similarity hypothesis, where species with similar traits limit invaders. In fact, the *Chenopodium* monoculture treatment had the lowest level of reinvasion, suggesting that a sampling effect may explain these patterns. *Chenopodium* grows quickly, grows large, and occupies space limiting reinvasion.

Soil water potential
Soil water potentials varied over time ($F_{21,1543} = 16.70$, $p<0.001$) and were lower (drier) in open, compared to shaded plots ($F_{1,1543} = 73.45$, $p<0.001$; Fig. 58a). Water potentials also varied significantly among species treatments ($F_{6,1543} = 6.18$, $p<0.001$; Fig. 58b). Water potential was highest in control, *Eragrostis*, and *Pennisetum* plots; intermediate in *Dodonaea* and *Chenopodium* plots, and lowest in the Chenopodium/*Eragrostis and Chenopodium/Dodonaea* treatments. None of the treatments significantly lowered soil water potential below that of *Pennisetum setaceum* (Fig. 58).

Pennisetum setaceum biomass

Total, live, and dead biomass of *Pennisetum setaceum* did not differ significantly among shaded treatments (paired t-test, p>0.3; Fig. 59). There was no difference in live:dead ratio of biomass between shade treatments (paired t-test, p>0.3).

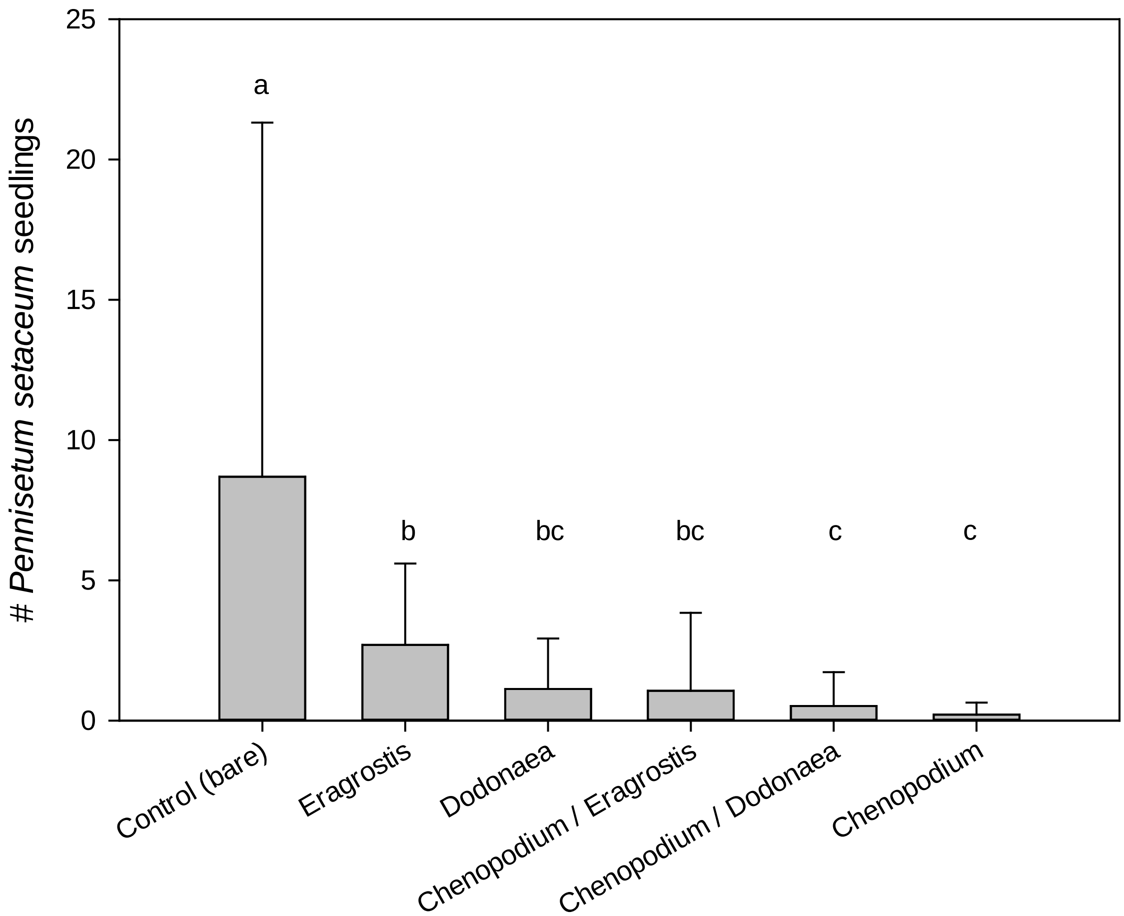


Figure 57. *Reinvasion measured as the number of Pennisetum setaceum individuals per plot.*

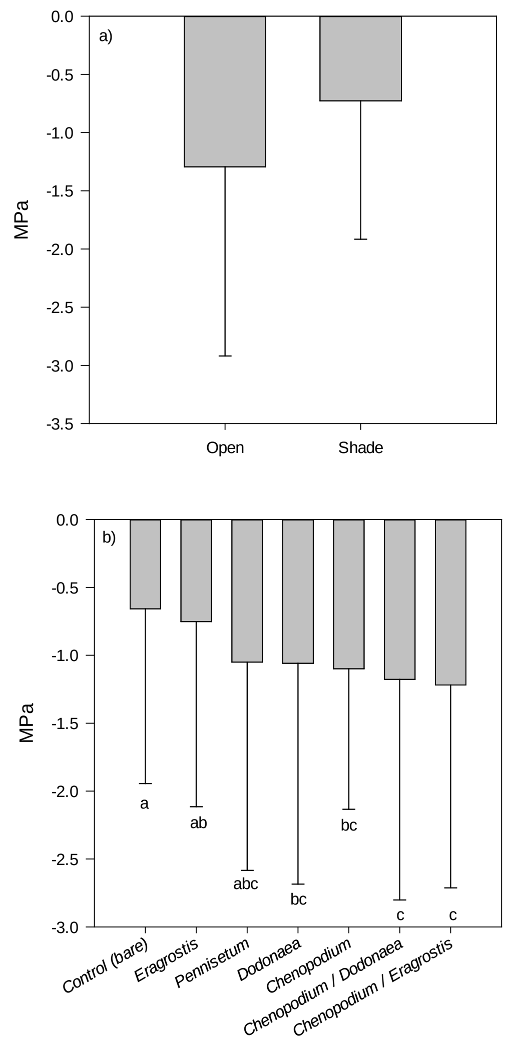


Figure 58. *Soil water potential in A) open versus shade treatments and B) species treatments.*

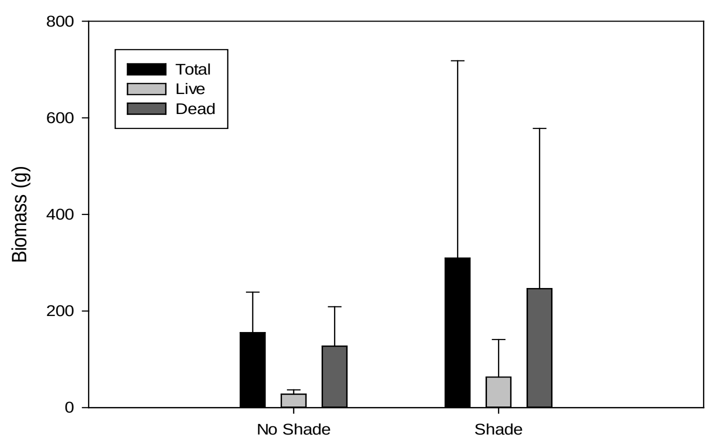


Figure 59. *Pennisetum setaceum biomass measured in Pennisetum plots at the end of the experiment to analyze grass fine fuels.*

5. Conclusions and Implications for Future Research/Implementation

5.1. General Conclusions

Our study was designed to provide basic scientific information and practical tools for managing and restoring tropical dry forest landscapes on military lands in the Pacific. We used remote sensing and field-based experiments to explore the prevalent drivers and threats of tropical dry forest degradation. In turn, we used the same approach to offer science based solutions towards the protection and recovery of these ecosystems. Further, we developed planning tools and techniques to prioritize landscapes so that they are compatible for multiple uses. This management strategy enables the installation to conduct training while conserving the natural resources upon which the quality of training ultimately depends. We expect that our results will be applied throughout Hawaii and in other areas where similar methodology and/or knowledge of similar fuels can be used.

Through remote sensing we assessed the historical and current condition of the two major dry forest landscapes on the island of Hawaii and provide information to assess their restoration potential. Products include historical maps of dry forest cover change and state-of-the-art high resolution maps of vegetation cover, species dominance, and fire fuel cover for purposes of setting a clear baseline for potential restoration efforts. To improve our understanding of altered fire regimes and devise methods to break the grass/wildfire cycle, we used both remote sensing and field based experiments. At the landscape scale, we developed a high temporal frequency satellite imagery web-based tool to monitor near real-time fire fuel conditions. Our field experiments were designed to simultaneously develop strategies for restoration of native species and test the effectiveness of restoration as a tool to reduce fine fuel loads and potential fire danger. Finally, our greenstrip design and results offer promise that these methods can be used to protect remnant dry forest fragments from large fires moving across landscapes dominated by invasive grasses. These approaches hopefully provide important information for breaking the grass/wildfire cycle and restoring native plants within degraded dry forest landscapes.

One of the objectives in our proposal was to combine newly developed remote sensing approaches with field based studies to define the current condition and historical changes to tropical dry forest ecosystems in Hawaii. We used aerial photography from 1954 and airborne LiDAR and imaging spectroscopy from 2008 to infer changes in extent and location of tall stature woody vegetation (tall trees, mostly *M. polymorpha*) in 127 km^2 of subalpine dry forest on the island of Hawaii (Pohakuloa Training Area). Overall the total percentage of forest cover did not change substantially but at least a third of the total area underwent woody vegetation change (tall woody and short woody). Further, spatial patterns suggest that fires may be the primary driver of reductions in woody vegetation cover. Small increases in forest cover were also detected and could be due to regeneration of dry forest trees or measurement errors associated with historical imagery. Areas remaining in woody vegetation cover over the 53-yr study interval can be targeted for restoration and management. We also provided an overview of the challenges associated with the integration of historical photography with contemporary conservation and management in Hawaii and the Pacific and suggest additional studies that would help to improve estimates.

In addition to analyses of historical aerial photography, we conducted soil surveys on old Mauna Kea substrates to determine whether contemporary dominance of the native C3 shrub *Dodonaea viscosa* is a recent phenomenon that could be facilitated by a grass fire cycle. We quantified the relative abundance of $\delta^{13}C$ isotopes in wood, charcoal, and soil organic matter among depth profiles and between sites with different contemporary abundance of C3 and C4 vegetation. As a result, we were able to determine that the C3/C4 composition of the vegetation community has changed quite dramatically through time. This may indicate a historic native grass-fire cycle.

The second component of our remote sensing objectives were to generate state-of-the-art high resolution maps of vegetation cover, species dominance, and fire fuel cover for purposes of setting a clear baseline for potential restoration efforts. A key component of this approach is the Carnegie Airborne Observatory (CAO), an integrated remote sensing and analysis system developed to support large-scale studies of the structural and biochemical properties of vegetation and ecosystems. Measurements from the CAO can guide field studies in the context of regional patterns, and provide insights over large areas that can help generate better management decisions.

Specifically, we analyzed the topography and canopy density from the CAO data combined with current microclimate measurements to identify areas with the greatest need for restoration and areas with high potential for restoration success. For example, areas in need of restoration had high invasive species cover, low native species cover, or conditions favorable to the spread of wildfire. Areas with high potential for restoration success had conditions favorable for plant growth, such as reduced wind speeds, greater water availability, and greater shade. We developed restoration planning tools for three dryland ecosystems that reflect different restoration targets, including biodiversity, endangered plant populations, ecosystem services, and fuel prevention.

The final spatially derived element of our project was to enhance the predictive capability of when fires will occur, we developed the use of high temporal frequency satellite imagery to monitor near real-time fire fuel conditions. Invasive grasses fuel fires in Hawaii because they are perennials, and thus they maintain a large amount of aboveground biomass throughout the year. Because these fuels differ noticeably from their mainland counterparts, traditional fire danger rating systems have not been effective in Hawaii. Our fuel fire web tool is available to DoD and other Hawaii based land managers.

The effectiveness of the restoration experiment treatments were measured as native plant survival, increases in native species cover, decreases in fuel loads and changes in microclimate. Our initial ideas hypothesized that native plant restoration would alter the micro-climate of the system such that total invasive grass biomass would decrease and that the live:dead ratio would increase. This is based on the premise that invasive C4 grasses need high light levels for maximum growth, and that shaded environments increase the live:dead ratio and thereby decrease flammability of a system. While this result was found in our field based experiments – and in particular the greenstrip experiment - a main finding was that the effect of habitat suitability and restoration treatments on measures of restoration effectiveness varied across sites, suggesting that restoration prescriptions should change across a productivity gradient. Sites at high productivity require active restoration to remove invasive species that contribute to fuels,

sites at low productivity require active restoration that increases resource availability and reduces environmental harshness, and passive restoration may be more effective at moderate productivity.

The purpose of the greenstrip study was to test a tool that has been used in parts of the arid continental United States to protect high value ecosystems from fire. In our case we wanted to identify species for restoration that would not only reduce the incidence of invasive grasses and thus fire in dryland ecosystems but would also resist invasion once in place. Our functional trait approach elucidated several high value species to be used for this approach and our treatments effectively reduced the likelihood of invasive grass re-invasion into the site. It is curious why in this component of the project we were able to definitively show a strong correlation between restoration treatments and the reduction of fine fuel loads whereas the results were more obscure in the restoration experiment. A major difference between the two was the starting point of the ecosystem prior to the implementation of the experimental design. In the greenstrip project we completely bulldozed the site prior to outplanting thereby removing multiple potential legacy effects of prior conditions. Further, the bulldozing disturbance used to create traditional fuel breaks will favor fountain grass reinvasion due to the changes to substrate that increase water availability and recruitment opportunities for foundation grass (Questad et al. 2012). Therefore, we hypothesized that greenstrips with established native species would deter the reinvasion of fountain grass due to the preemption of space and resources, and thus reduce the maintenance required to remove grass fuels. Overall, greenstrips appear be a favorable technique to reduce fuel loads in degraded habitats.

In summary, this comprehensive research program has provided basic scientific information and practical tools for managing and restoring tropical dry forest landscapes in the Pacific. Results benefit the military mission in the Pacific by increasing capacity and knowledge to restore native forests, thereby reducing wildfire and enhancing habitat for threatened and endangered species.

5.2. Implementation

The products that have been developed for this work have already been incorporated into natural resource planning for PTA and other land management agencies in the state. Products from the habitat suitability model effort include the attainment of an ESTCP award to further validate the approach and model using field demonstrations and readily available satellite imagery. Results from this project have also catalyzed 2 important efforts related to altered fire regimes; 1) we have secured funding to expand our fire modeling efforts at PTA to include scenario building comprising the anticipated role of climate change on fire in dry systems in Hawaii; and 2) the formation of the Pacific Fire Exchange – A means of transferring knowledge between scientists, resource managers, decision-makers, fire suppression agencies, and communities in Hawaii and the U.S. affiliated Pacific and a structured forum and process for identifying and prioritizing critical new areas of fire research. The consortium was recently funded (December 2015) by the Joint Fire Science Program. The Hawaii DoD (from PTA, Makua, and Schofield) is listed on the proposal as a project coordinator. We are continuing to collect data from our restoration experiment to monitor longer term outcomes of restoration in correlation with interannual climate variability.

Our initial investment with the Carnegie Airborne Observatory (CAO-1) facilitated island wide research in association with fellow Forest Service scientists at IPIF resulting in 21 IPIF associated peer reviewed publications in addition to several management tools for planning large-scale restoration actions and managing fire danger. These flights allowed for first ever landscape-scale mapping of invasive species presence, fuels and fuel moisture conditions, aboveground carbon stocks, and structural forest properties that support native bird and insect species. In January 2016 the IPIF-Carnegie team completed a large-scale remapping of Hawaii Island. The mapping will target all major forested areas, from wet to dry and from lowland to treeline. Mapping will primarily focus on forests that were previously assessed for species composition, carbon stock and functional traits during 2007-2008 overflights. PTA was very supportive of this re-flight the process of securing funds to support a re-analysis of the PTA landscape.

5.3. Implications for Future Research

Overall, this DoD supported research program has served as an important catalyst for generating the necessary science to help address important natural resource management needs for Hawaii and the Pacific. Given that the budgets associated with implementing DoD natural resource management plans are estimated to be several million dollars, tools to reduce the cost of these activities while promoting the maintenance, protection and enhancement of dry forest communities are key. Ideally, results from this study will both influence, and be incorporated into revised Integrated Natural Resource and Wildfire Management Plans for PTA and other DoD installations in Hawaii and the Pacific. Further, the establishment of field and lab based research infrastructure provide opportunities to expand our understanding of these valuable ecosystems. Below we highlight several key areas of our research with expansion opportunities.

MODIS Web Tool
The National Fire Danger Rating System (NFDRS) indices are key components of any region's Wildfire Management Plan. In Hawaii, as elsewhere, these indices are computed from weather observations taken by Remote Automated Weather Stations (RAWS). Hawaii's mix of climate and fuel types have yet to be effectively captured in NFDRS because standard fuel moisture models tend to be poor predictors of on-the-ground fuel moistures and Hawaii's climate allows for year round vegetation growth and fire risk. These factors make the calculation of meaningful NFDRS indices challenging in Hawaii, greatly complicating fire management. The Hawaii Vegetation Fire Risk web tool (http://hawaiifire.stanford.edu/) which maps the proportions of Photosynthetic Vegetation (PV), Non-Photosynthetic Vegetation (NPV), and Barren (B) ground across Hawaii county at 500m spatial and 8-day temporal resolutions may offer a novel solution for land managers to plan for wildfire. To the extent that NPV represents dead vegetation and not the stems of woody material, it can ideally track vegetation phenology as it responds to pulses of rainfall, and therefore, track changes in fine fuel moisture, a primary driver of fire ignition and spread. If this tool proves effective for monitoring fire danger in Hawaii, it will represent a significant advance on previously available methods (e.g., micrometeorological approaches) because MODIS coverage is more spatially extensive and potentially more relevant to the Hawaiian fire environment than current NFDRS indices.

Long Term Impacts of Restoration on Fuel Modeling

While early results from these studies have provided valuable information on native plant establishment and survival, our restoration project success is highly dependent on site suitability. While we have provided insights into the potential for interrupting the grass-wildfire feedback cycle, we believe that they may not necessarily be indicative of longer-term treatment effectiveness. Specifically, we hypothesize that as treatments mature (*i.e.* longer time periods of rest from feral ungulate herbivory and trampling, growth of native plants), there will be greater suppression of invasive grasses, increased fuel moisture of surface fuels due to shading by canopy species, and thus, impacts of restoration treatments on potential fire occurrence and behavior that were not documented in the first several years of measurements. Further, we expect a greater influence of inter- and intra-annual climate on treatment success that we were able to document in initial measurements. Dry ecosystems in Hawaii experience large interannual climate variation, resulting in significant variability in fuel loads and fire risk. During our initial experiments, Hawaii was in a period of severe and prolonged drought. In the past two years, in contrast, the islands have experienced above average rainfall. Our observations of site conditions in recent years show large reductions of invasive grass and positive responses of native plants to this increased rainfall. With longer term data on restoration treatments Structural Equation Models (SEM) could be used to test the strength and direction of different ecological controls on plant community type. SEM are based on regression analyses, but can incorporate networks of causal relationships to confirm postulated relationships among variables. If models that arise out of SEM analyses are robust then key controlling processes as identified by SEM can be manipulated to alter successional trajectories in invaded communities.

Impacts of Fire on Belowground Processes

The belowground implications of non-natural fire regimes in Hawaii is not widely studied. Evidence elucidated in this study following a large anthropogenic fire indicated reduced soil nutrient availability perhaps due to losses from volatilization and wind (ash removed post fire) and via post-fire regeneration by a novel assemblage of non-native species. It appears, therefore, that fire in this ecosystem is destructive both above and below ground. The direct and indirect effects of fire may also damage critical plant-soil interactions such as symbiotic relationships with mycorrhizal fungi. We speculate that fire in this system alters soil microbial communities and nutrients in a way that leads to reduced capacity for native woodland species regeneration.

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7. Appendices

A. Supporting Data

1. The role of high intensity fire on tropical dry ecosystems – mycorrhizal associations

Research has shown that a fire can permanently alter the successional pathway of Hawaiian dry forest ecosystems. In addition to lethal damage from fire, many native plants also have difficulty regenerating after an area is burned. Fire can disrupt soil structure, sterilize the seed bank, volatilize critical nutrients, and damage mycorrhizal fungal associations. An area that supported a diverse forest before a fire is most likely to succeed into a shrubland dominated by *Dodonaea viscosa* and invasive grasses and forbs. Experiments have shown that broadcast of seeds, especially when coupled with a regular watering schedule, can result in the reestablishment of some native species. The most successful native species in post-burn conditions is aweoweo (*Chenopodium oahuense*). Members of the Chenopodiaceae are known not to form mycorrhizal associations with soil fungi. Some native species that were displaced by the fire such as mamane (*Sophora chrysophylla*) are known to be strongly associated with mycorrhizae and have not become reestablished, even after seeding and watering. With additional funding received from SERDP we used standard techniques to identify the mycorrhizal associations in several plant communities on Mauna Kea following the devastating fire at PTA in 2012. The results in Table 13 indicate the importance of mycorrhizae in ecosystem restoration. In 2016 we will incorporate these results into a new experimental design addressing the relationship between mycorrhizae and key plant nutrients.

Table 13. Mycorrhizal associations with common dry forest plants

Non mycorrhizal species

Species	*Type*	*Origin*
Eragrostis atropioides	grass	native
Nassela cernua	grass	nonnative
Lepidium virginianum	forb	nonnative
Portulaca pilosa	forb	nonnative
Chenopodium oahuense	shrub	native
Grevillea robusta	tree	nonnative

Highly mycorrhizal species

Species	*Type*	*Origin*
Pennisetum setaceum	grass	nonnative
Verbesina encelioides	forb	nonnative
Bidens menziesii	shrub	native
Lantana camara	shrub	nonnative
Ricinus communis	shrub	nonnative
Sophora chrysophylla	tree	native
Delairea odorata	vine	nonnative

Species with **Moderate** levels of mycorrhizal inoculation

Species	*Type*	*Origin*
Dodonaea viscosa	shrub	native
Euphorbia olowaluana	tree	native
Myoporum sandwicensis	tree	native
Jacaranda mimosifolia	tree	nonnative

Species with variable to **Low** levels of mycorrhizal inoculation

Species	*Type*	*Origin*
Melinis	grass	nonnative
Plectranthus parviflora	forb	native
Erodium cicutarium	forb	nonnative
Senecio madagascariensis	forb	nonnative
Nicotiana glauca	shrub	nonnative

2. Micrometeorology Data

We explored microclimate differences among suitability classes (high and low) at each of the three forest types. We installed weather stations in February 2010 in each plot that logged measurements of air temperature, relative humidity, and wind speed every minute, in addition we measured rainfall and soil moisture in the low suitability site (because it was more open) within each forest type (Onset Computer Corporation, Pocasset, Massachusetts, USA). We lacked replication for statistical analysis of these intensive measurements and display the results graphically.

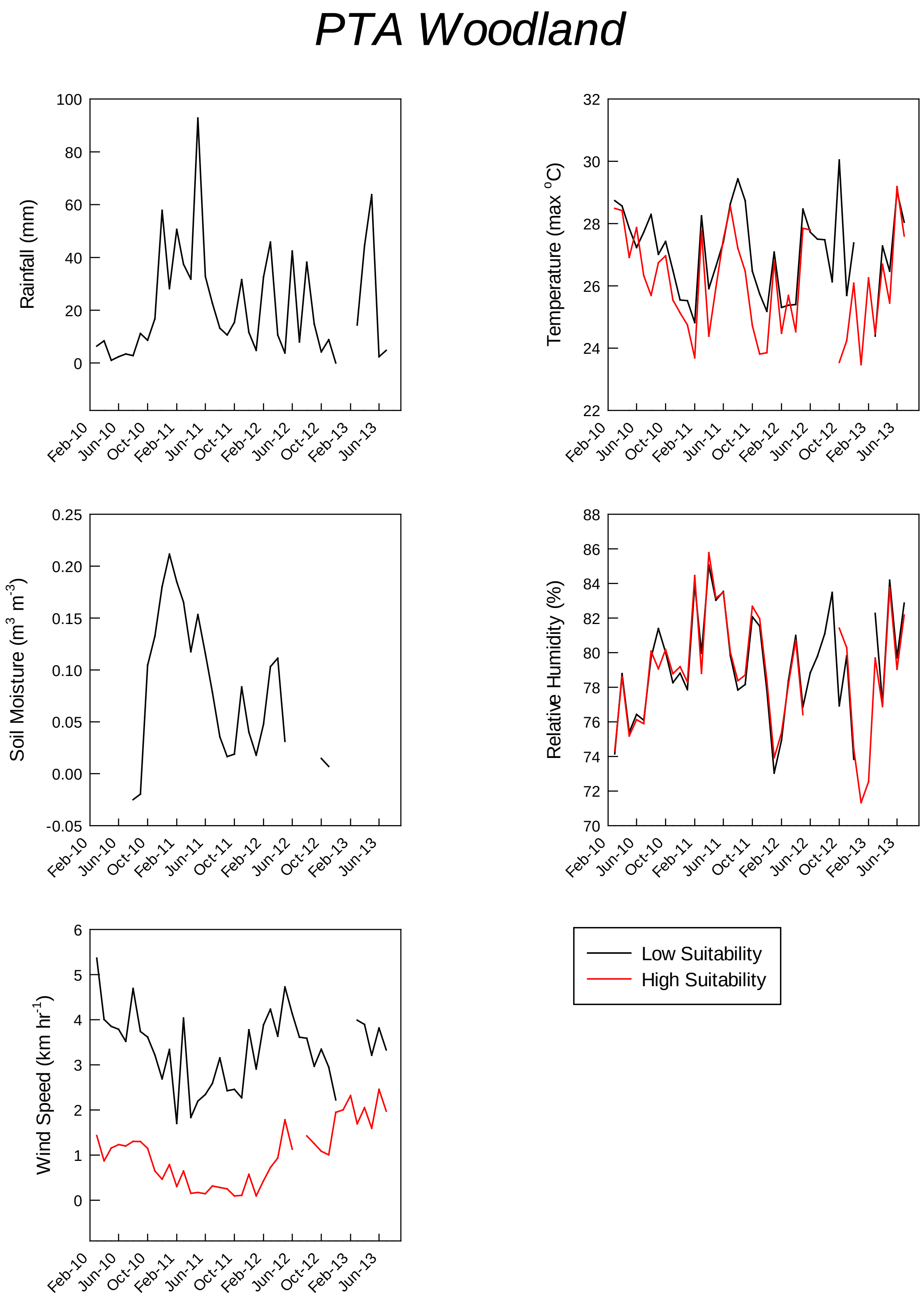

Figure 60. *Micrometeorological data for the PTA Woodland*

PTA Shrubland

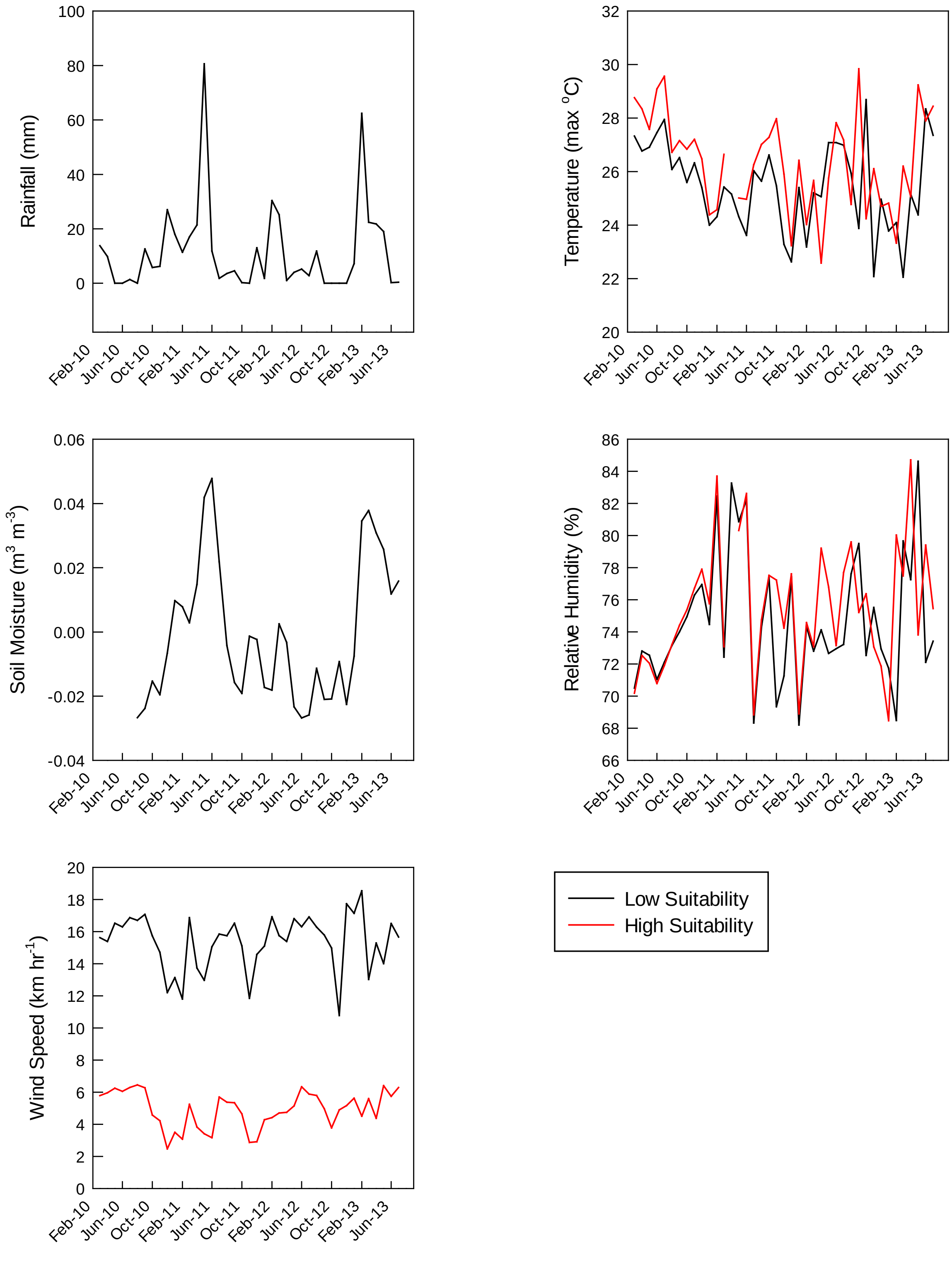

Figure 61. *Micrometeorological data for the PTA Shrubland*

PWW Woodland

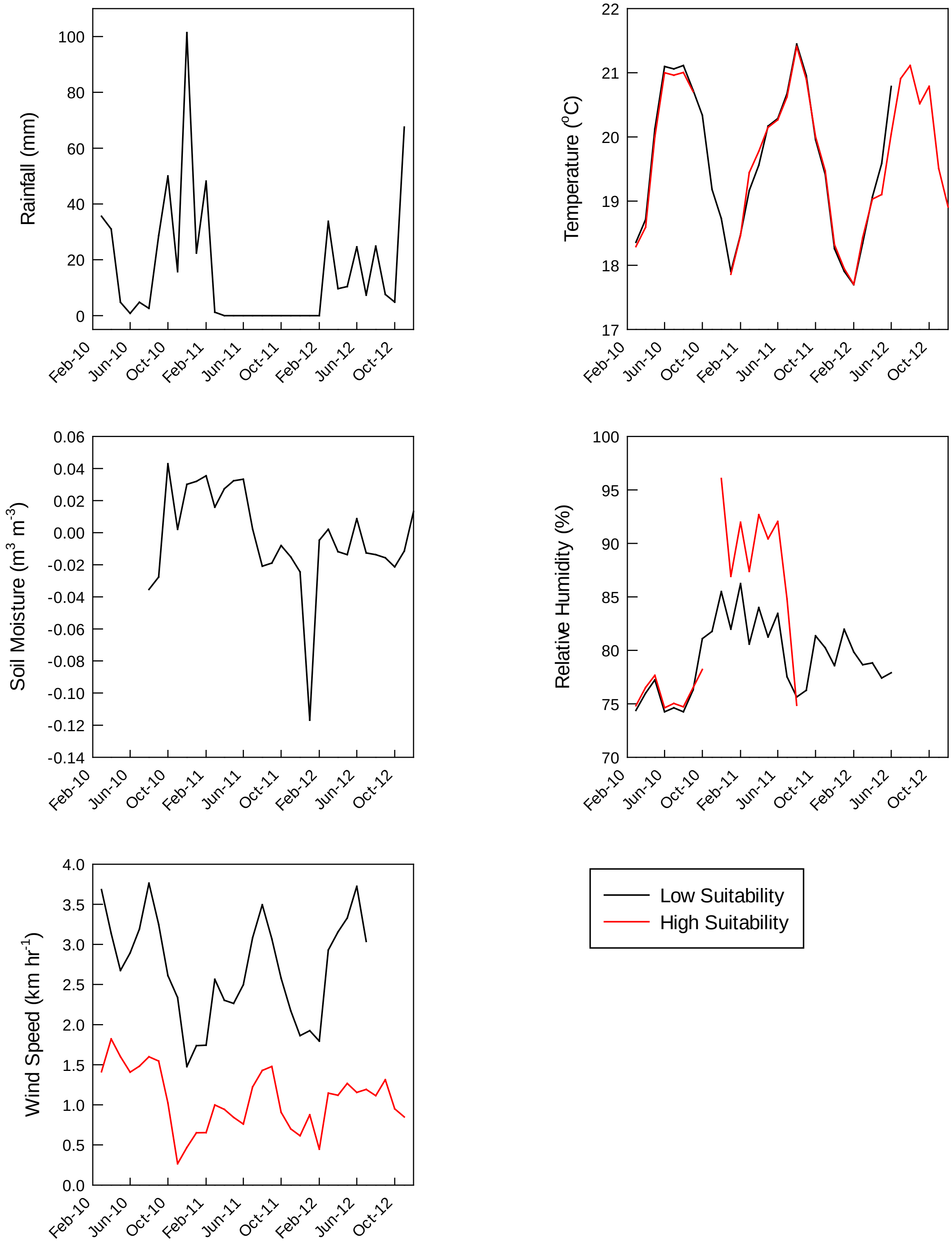

Figure 62. *Micrometeorological data for PWW Woodland*

B. List of Scientific/Technical Publications

2008

Cordell, S. Asner, G.P., Thaxton, J., Kellner, J.R., Knapp, D.E., Kennedy-Bowdoin, T., Ambagis, S. Kinney, K.M., Questad, E., Selvig, M., Biggs, M., and Johansen, J. 2008. The Potential for Restoration to Break the Grass/Fire Cycle in Dryland Ecosystems in Hawai`i. SERDP/ ESTCP Partners in Environmental Technology Technical Symposium & Workshop, December 2-4. Washington D.C. (Published Abstract)

2009

Cordell, S., Asner, G.P., Thaxton, J. The Potential for Restoration to Break the Grass/Fire Cycle in Dryland Ecosystems in Hawai`i. SERDP 2009 Annual Report. Submitted February 12, 2009.

Kellner, J.R., Asner, G.P., Kinney, K.M., Loarie, S.R., Knapp, D.E., Kennedy-Bowdoin, T., Questad, E., Cordell, S., and Thaxton, J.M. 2009. Seasonal dynamics and woodland community type regulate the fire fuel properties of the invasive grass *Pennisetum setaceum.* SERDP/ ESTCP Partners in Environmental Technology Technical Symposium & Workshop, December 1-3. Washington D.C. (Published Abstract)

Questad, E.J., S. Cordell, and D. Sandquist. Functional diversity and invasive species in Hawaiian forests. The 10th International Congress of Ecology. Brisbane, Australia. August 16-21, 2009. (Published Abstract)

2010

Thaxton, J.M., Cole, T.C., Cordell, S., Cabin, R.J., Sandquist, D.R., and Litton, C.M. 2010. Native species regeneration following ungulate exclusion and non-native grass removal in remnant Hawaiian Dry Forest. Pacific Science. 64, 533-544. (Refereed Journal Article)

Chynoweth, M.W., Litton, C.M., Lepczyk, C.A., Cordell, S., and Kellner, J.R. 2010. Movement Ecology of Nonnative Feral Goats in Hawaiian Dryland Ecosystems. The Wildlife Society Conference, Snowbird, UT (Poster abstract)

-Vertebrate Pest Conference: February 2010, Sacramento, CA. (Published Abstract)
-Hawaii Conservation Conference: August, 2010, Honolulu, HI (Published Abstract).

Cordell, S., Asner, G.P., Thaxton, J. The Potential for Restoration to Break the Grass/Fire Cycle in Dryland Ecosystems in Hawai`i. SERDP 2009 Annual Report. Submitted February 1, 2010.

Cordell, S., Kellner, J.R. 2010. The Potential for Restoration to Break the Grass/Fire Cycle in Dryland Ecosystems in Hawai`i. DoD Pacific Islands Threatened, Endangered, and At-Risk Species Workshop II, February 2-4, 2010. Honolulu, HI (Published Abstract)

Cordell, S. Restoration of ecosystems invaded by arid perennial grasses. Western Society of Weed Science, 2010 Annual Meeting. Waikoloa, HI. (Invited oral presentation, published abstract).

Kellner, J.R. 2010. Remote sensing landscape fuel loads and an annual forb invasion. Western Society of Weed Science, 2010 Annual Meeting. Waikoloa, HI. (Invited oral presentation, published abstract).

Kinney, K.M., Kellner, J.R., Selvig, M., Asner, G.P., Cordell, S., Questad, E., Thaxton, J.M. Knapp, D.E., Kennedy-Bowdoin, T. 2010. An Eye on Restoration: New Remote Sensing Approaches that Change the Way We See Dryland Ecosystem Restoration in Hawai`i. Environmental Management Publication. Volume 49, pg 4-5. (Non-Refereed Article)

Kinney, K.M., Asner, G.P. Kellner, J.R., Knapp, D.E., Kennedy-Bowdoin, T., Questad, E.J., Cordell, S., Thaxton, J.M. Remote sensing of potential restoration in a Hawaiian subalpine dry forest. Ecological Society of America Annual Meeting (2010), Pittsburgh, PA. (Published Abstract)

Moseley, R., Selvig, M., Questad, E., Cordell, S., and Thaxton, J. Restoration Potential of Three Hawaiian Dryland Ecosystems. 2010. Hawaii Conservation Conference, Honolulu, HI, (Published Abstract)

Questad, E.J., J. Kellner, K. Kinney, S. Cordell, J. Thaxton, and G. Asner. 2010. Increasing the impact and success of ecological restoration in Hawaiian dryland ecosystems. Partners in environmental technology technical symposium, US Department of Defense (Published Abstract).

Questad, E.J., J. Thaxton, and S. Cordell. 2009. Invasion resistance in Hawaiian tropical dry forests. Ecological Society of America (Published abstract).

2011

Kellner, J.R., Asner, G.P., Kinney, K.M., Loarie, S.R., Knapp, D.E., Kennedy-Bowdoin, T., Questad, E., Cordell, S., and Thaxton, J.M. 2011. Remote analysis of biological invasion and the impact of enemy release. Ecological Applications. 21(6) 2094-2104. (Refereed Journal Article)

Chynoweth, Mark; Litton, Creighton M.; Lepczyk, Christopher A.; Cordell, Susan. 2010. Feral goats in the Hawaiian Islands: understanding the behavioral ecology of nonnative ungulates with GPS and remote sensing technology. In: Timm, R.M.; Fagerstone, K.A., eds. Proceedings of the 24th Vertebrate Pest Conference; 2010, 41-45. (Refereed Journal Article)

Cordell, Susan; Asner, Greg P.; Thaxton, Jarrod 2011. The potential for restoration to break the grass/fire cycle in dryland ecosystems in Hawai`i. SERDP 2010 Annual Report.

Chynoweth, Mark W.; Lepczyk, Chris A.; Litton, Creighton M.; Cordell, Susan. 2011. Movement patterns and habitat utilization of nonnative feral goats in Hawaiian dryland montane landscapes. Ecological Society of America Annual Meeting; 2011 August 7-12; Austin, TX. (Published abstract)

-Hawaii Conservation Conference--Island Ecosystems: The Year of the Forest; 2011 August 2-4; Honolulu, HI. Honolulu, HI: Hawaii Conservation Alliance: 39. (Published abstract). ***awarded best student presentation of the conference***

-US Chapter of the International Association for Landscape Ecology 2011 Annual Symposium; 2011 April 3-7; Portland OR. Frostburg, MD; US-International Association for Landscape Ecology. (Published abstract)

Chynoweth, Mark 2011. Feral goats in Hawaiian dryland ecosystems - ecology and impacts. Nahelehele Dry Forest Symposium, February 25, 2011, Kailua-Kona, HI (Invited oral presentation).

Cordell, Susan; Questad, Erin J.; Kinney, Kealoha; Kellner, James R.; Thaxton, Jarrod; Asner, Greg P. 2011. Guiding ecological restoration in invaded landscapes. In: 96th Ecological Society of America Annual Meeting, 2011 August 7-12; Austin, TX. (Poster abstract)

Cordell, Susan; Giardina, Christian; Nakahara, Miles; *Pickett Fee, Elizabeth; Stewart, Carolyn 2011. Development of Hawaii and U.S. Affiliated Pacific Island Fire Science Consortium. In: 2011 Hawaii Conservation Conference--Island Ecosystems: The Year of the Forest; 2011 August 2-4; Honolulu, HI. Honolulu, HI: Hawaii Conservation Alliance: 73. (Poster Abstract).

Questad, Erin J.; Cordell, Susan; Kinney, Kealoha; Kellner, James R.; Thaxton, Jarrod; Asner, Greg P. 2011. Guiding ecological restoration in invaded landscapes. In: US Chapter of the International Association for Landscape Ecology 2011 Annual Symposium; 2011 April 3-7; Portland OR. Frostburg, MD; US-International Association for Landscape Ecology.(Published abstract).

Questad, Erin J.; Cordell, Susan; Thaxton, Jarrod. 2011. Invasion and native species loss through local extinction. In: 96th Ecological Society of America Annual Meeting, 2011 August 7-12; Austin, TX. (Published abstract)

2012

Questad, E., Thaxton, J.M., Cordell, S. 2012. Patterns and consequences of re-invasion into a Hawaiian dry forest restoration. Biological Invasions 14:2573-2586. (Refereed Journal Article)

Thaxton, J.M., S.Cordell, R.J. Cabin and D.R. Sandquist. 2012. Non-native grass removal and shade increase soil moisture and seedling performance during Hawaiian dry forest restoration. Restoration Ecology. 20 (4) 475-482. (Refereed Journal Article)

Kellner, J.R. Asner, G.P., Ambagis, S., Cordell, S., Thaxton, J, Kinney, K.M., Kennedy-Bowdoin, T., Knapp, T., Questad, E. 2012. Historical Land-Cover Classification for Conservation and Management in Hawaiian Subalpine Drylands. Pacific Science 66: 457-466. (Refereed Journal Article)

Cordell, S., Asner, G., Thaxton, J., Questad, E., Kellner, J., Kinney K., Chynoweth, M., Brooks, S. and Uowolo, A. 2012. The Potential for Restoration to Break the Grass / Fire Cycle in Dryland Ecosystems in Hawaii. USFS-Pacific Southwest Research Station Brochure. (Brochure)

Cordell, S., Kellner, J.R., Questad, E., Asner, G.P., Kinney, K.M., Loarie, S.R., Knapp, D.E., Kennedy-Bowdoin, T., Uowolo, A., and Thaxton, J.M. 2012. Practical tools for managing and restoring tropical dry forest landscapes on military lands in the Pacific. 5th Annual Fire Ecology and Management Congress. December 3-7. Portland OR. (Published abstract)

Kinney, K., Kellner, J., Cordell, S., Asner, G.P., Thaxton, J., Questad, E., Knapp, D., Kennedy-Bowdoin, T., and Hall, L. 2012. Fire regime facilitates unexpected nutrient limitation in Hawaiian subalpine dry forest? 5th Annual Fire Ecology and Management Congress. December 3-7. Portland OR. (Published abstract)

Kinney, K.M., Kellner, J.R,. Asner, G.P., Chadwick, O.A., Cordell, S., Heckman, K., Hotchkiss, S., Jeraj, M., Kennedy-Bowdoin, T., Knapp, D.E., Questad, E., Thaxton, J., Trusdell, F. 2013. Premature Decline of Ecosystem Structure and Plant-available Phosphorus on a Dryland Chronosequence in Hawaii. Hawaii Conservation Conference, July 16-18. Honolulu, HI (Published abstract)

Kinney, K., Kellner, J., Cordell, S., Asner, G.P., Thaxton, J., Questad, E., Knapp, D., Kennedy-Bowdoin, T., and Hall, L. 2012. Detecting a prehistoric fire regime in a Hawaiian sub – alpine dry forest. Ecological Society of America Annual Conference; August 5-10. Portland OR. (Published abstract)

Cordell, S., Asner, G., Thaxton, J., Questad, E., Kellner, J., Kinney K., Chynoweth, M., Brooks, S. and Uowolo, A. 2012. The Potential for Restoration to Break the Grass / Fire Cycle in Dryland Ecosystems in Hawaii. Hawaii Conservation Conference, July 31-Aug. 2. Honolulu, HI (Published abstract)

Questad, E., Cordell, S., Kellner, J., Brooks, S. 2012. Habitat suitability modeling for the restoration of threatened, endangered, and at-risk plant species in dryland ecosystems of Hawaii and Southern California. Hawaii Conservation Conference, July 31-Aug.2. Honolulu, HI. (Published abstract)

2013

Chynoweth, M.W., C.M. Litton, C.A. Lepczyk, S.C. Hess, and S. Cordell. 2013. Biology and Impacts of Pacific Island Invasive Species. Capra hircus, the Feral Goat, (Mammalia: Bovidae). Pacific Science. 7:141-156. (Refereed Journal Article)

Cram, D., Cordell, S., Giardina, C., Litton, C.M., Moller, E., Pickett, E., and Friday, J.B. 2013. Fire and Drought in Paradise – Say It Isn't So, Smokey. Rural Connections. 7:19-22. (Magazine Article)

Janas, D., Cordell, S., Uowolo, A., Thiet, R. 2013. Restoring Dryland Forests From the Soil Up. Hawaii Conservation Conference, July 16-18. Honolulu, HI (Published abstract)

Kinney, K.M., Kellner, J.R, Asner, G.P., Chadwick, O.A., Cordell, S., Heckman, K., Hotchkiss, S., Jeraj, M., Kennedy-Bowdoin, T., Knapp, D.E., Questad, E., Thaxton, J., Trusdell, F. 2013. Premature Decline of Ecosystem Structure and Plant-available Phosphorus on a Dryland Chronosequence in Hawaii. Hawaii Conservation Conference, July 16-18. Honolulu, HI (Published abstract)

Pierce, A., Cordell, S., Litton, C.M., Giardina, C. 2013. Examining Future Fire Weather Scenarios in Hawaii: Impacts of Future Climate Change on the Frequency of Severe Fire Weather Days. Hawaii Conservation Conference, July 16-18. Honolulu, HI (Published abstract)

Questad, E.J., J. R. Kellner, K. Kinney, S. Cordell, G. P. Asner, A. Uowolo, and S. Brooks.

Remote mapping of habitat suitability for at-risk plant species and its implications for restoration and reintroduction. Society for Ecological Restoration World Conference, October 6-11. Madison, WI (Published abstract).

2014

Questad, E., Kellner, J.R., Kinney, K**,** Cordell, S., Asner, G.P., Thaxton, J., Diep, J., Uowolo, A., Brooks, S., Inman-Narahari, N., Evans, S., and Tucker, B. 2014. Mapping habitat suitability for at-risk plants and its implications for restoration and reintroduction. Ecological Applications: 24:385-395 (Refereed Journal Article)

Cordell, S., E.J. Questad, J. R. Kellner, S. Brooks, A. Uowolo, G. Asner, and E. Parsons. 2014. Remote mapping of habitat suitability for at-risk plant species: implications for restoration and reintroduction. USFS-Pacific Southwest Research Station Brochure. (Brochure)

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Questad, E.J., S. Cordell, J. R. Kellner, G. P. Asner, S. Brooks, A. Uowolo, K. Kinney, and E. Parsons. Using topographic habitat suitability to reintroduce at-risk plant species. Hawaii Ecosystems Meeting, June 25-26, 2014. Hilo, HI. (Oral presentation)

S. Brooks, E. Questad, J. Kellner, S. Cordell, K. Kinney, A. Uowolo, E. Parsons, J. Thaxton, G. Asner. 2014. Habitat suitability modelling for the restoration of threatened, endangered, and at-risk plant species in dryland ecosystems of Hawaii and Southern California. Nahelehele Dry Forest Symposium, February 21. Kailua-Kona, HI. (Poster presentation)

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Other Technical Material - Awards

Cordell, S. 2008. Certificate of Merit, from the USDA Forest Service, Pacific Southwest Station "Advancing our Knowledge And Understanding of Tropical Dry Forests".

Cordell, S. 2010. Certificate of Merit, from the USDA Forest Service, Pacific Southwest Station "Achieving Forest Service Mission in Hawaii and the Pacific and especially for strong scholarship in restoration ecology and strong leadership in building partnerships in the establishment of the Hawaii Experimental Tropical Forest.

Our paper in Ecological Applications (Questad et al. 2014) was featured in Science as the Editor's Choice, Highlights of recent literature, Ecology-Data driven decision making. Science. 2014. Vol 344, Issue 6179:10.

C. Other Supporting Materials

1. Hawaii Vegetation Fire Risk WebTool

Purpose

The Hawaii Vegetation Fire Risk web tool is designed to assist Users with estimating vegetation-related fire risk on the Island of Hawaii.

Disclaimer

This experimental web tool can be freely accessed but at the sole risk of the User. The Carnegie Institution makes no warranty as to the quality and/or accuracy of any data obtained by the User of this tool. The User assumes all risks and liabilities in the interpretation and use of any data or results obtained from this experimental web tool.

Use

Using the webtool is easy. Simply click anywhere in the map and allow the time-graph to load in the upper right portion of your browser. Any missing data points in the time-graph are due to cloudiness in the satellite data record. By moving your mouse cursor over the time-graph, you can view vegetation conditions at any point in time for which there are satellite measurements (see below about satellite availability). You can also download the time-graph for your point using the "Download CSV for this point", which can be read in Microsoft Excel or compatible spreadsheet software.

Analysis Method

Vegetation fire risk maps are generated using a combination of NASA satellite data and Carnegie data processing methods. The information is generated only for Hawaii Island and is subject to the limitations of NASA-provided satellite imagery (see below).

The satellite data are automatically updated and processed approximately every 15 days. This frequency is set by NASA data availability. Each image is taken from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Terra satellite. The web tool ingests the MOD09A1 seven-band reflectance, 8-day composite, which is provided at 500 meter spatial resolution.

The MODIS reflectance data are processed to provide sub-pixel cover percentages (or fractions) spanning 0 to 100% for moist vegetation, dry vegetation, and bare rock/soil. For example, a dry vegetation fraction of 0.30 is 30% cover of dry fire-prone vegetation within the 500 x 500 meter MODIS pixel. The analysis is done using the *Automated Monte Carlo Unmixing* (*AutoMCU*) algorithm published by Asner and Heidebrecht (2001) and updated by Asner et al. (2005).

Limitations

Hawaii Island is a very cloudy region. As a result, most images are missing portions, and sometimes large areas, of the island. This is not an error in data processing. It is due to clouds in the MODIS data.

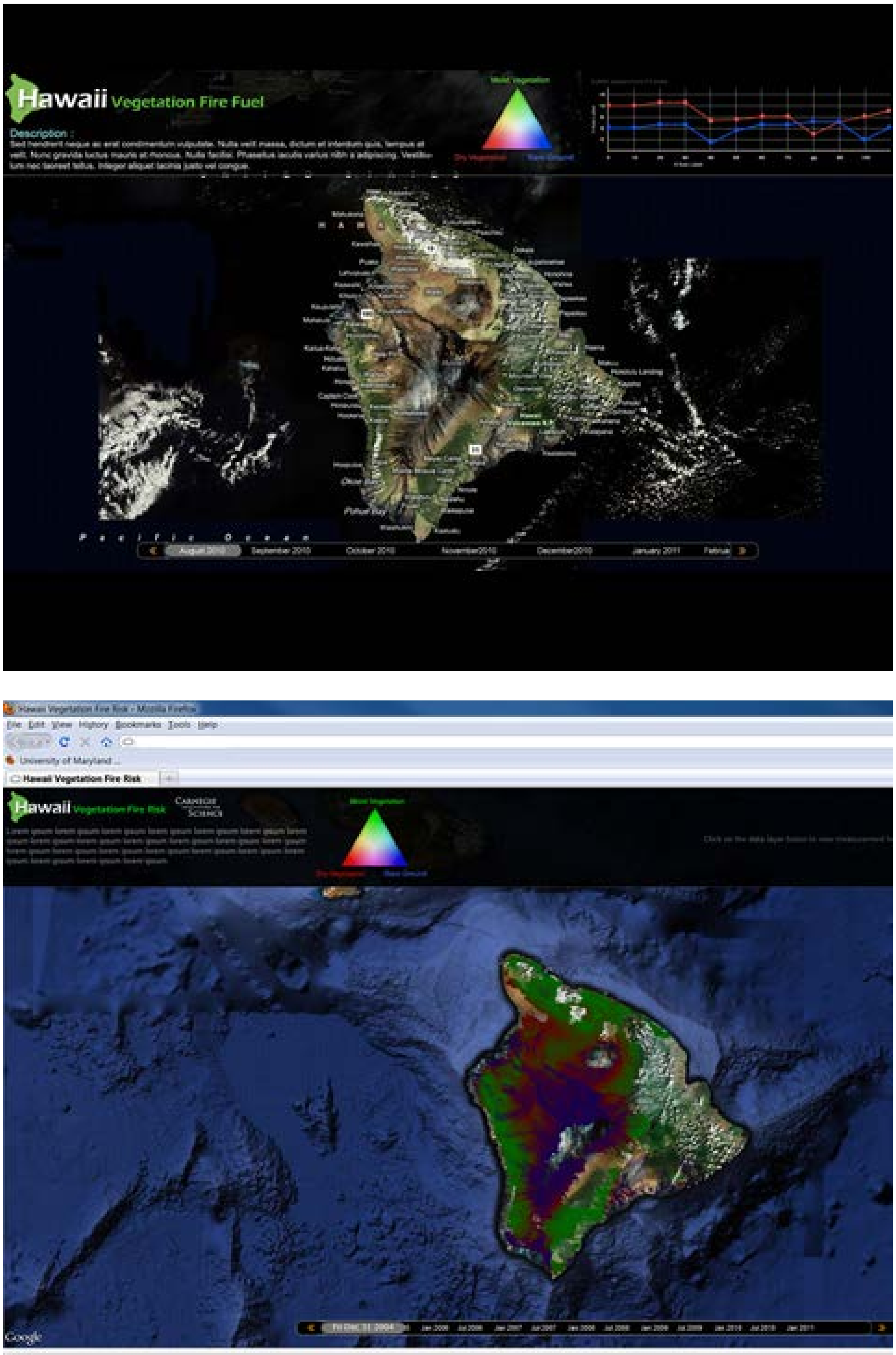
There are stripes in various locations in the images. This is not an error in data processing. It is due to errors in the NASA MODIS satellite compositing.

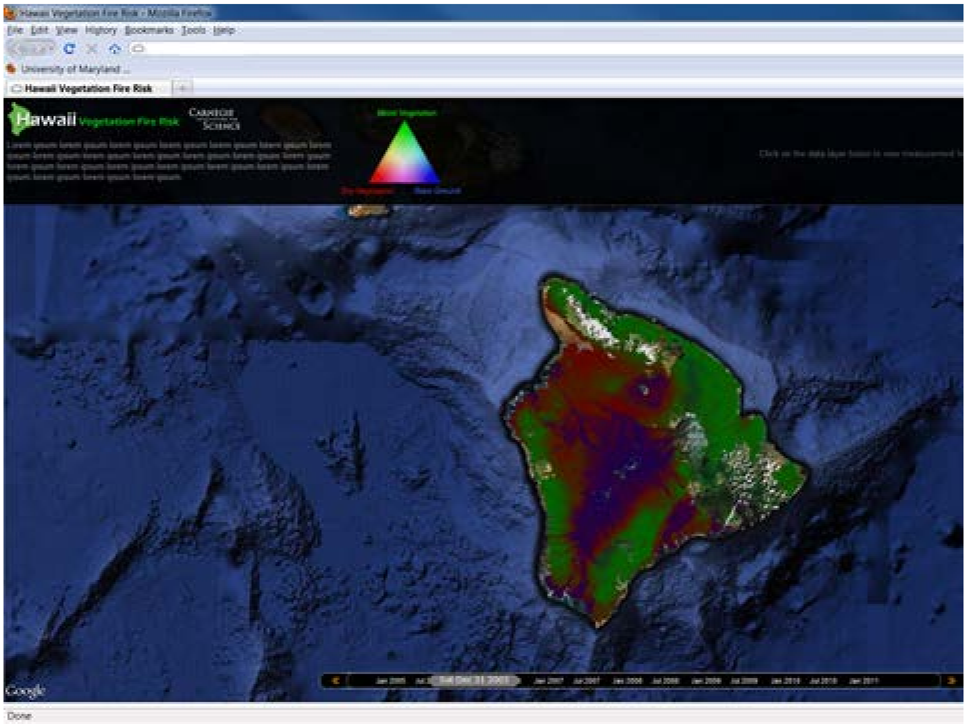
This project was supported by the Strategic Environmental Research and Development Program (www.serdp.org). For questions or suggestions, contact Greg Asner (gpa@stanford.edu) or Dave Knapp (deknapp@stanford.edu).

Figure 63. *Description of the Hawaii Vegetation Fire Risk Tool*

Demonstration of the Hawaii Vegetation Fire Risk WebTool

Figure 64. *Each figure pane represents the Island of Hawaii across inter- and intra-annual timescales. Note the variation in PV and NPV.*

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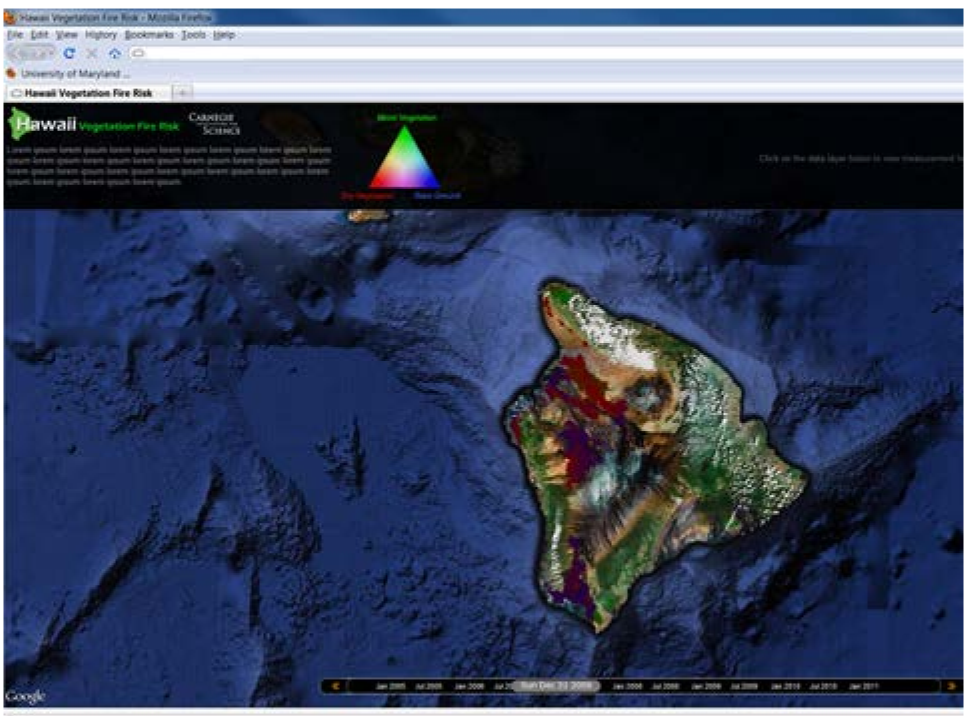
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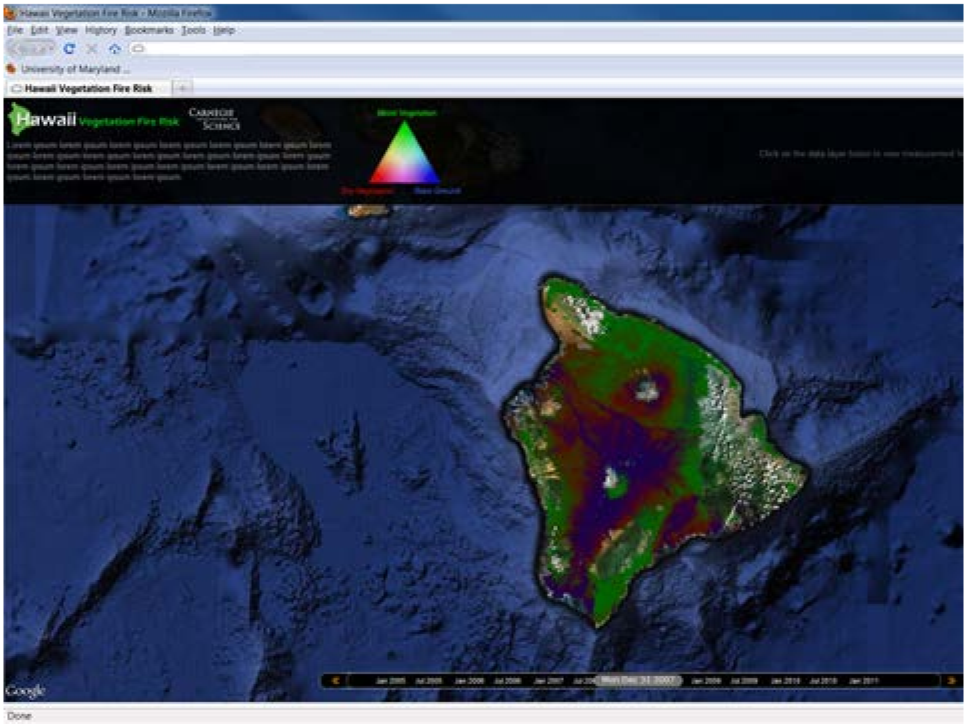
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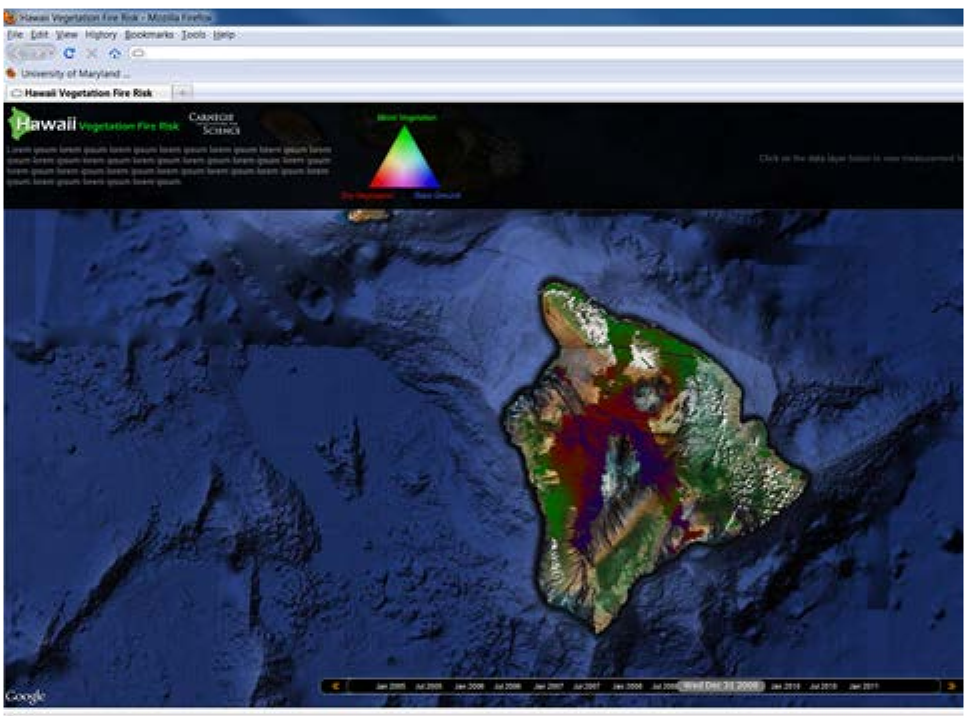
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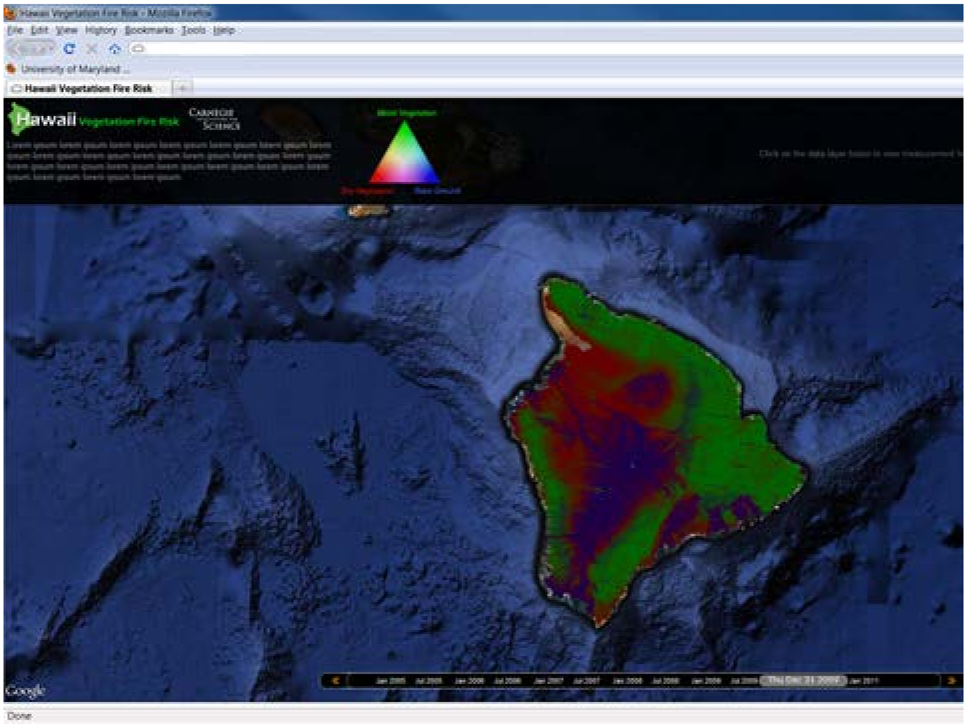

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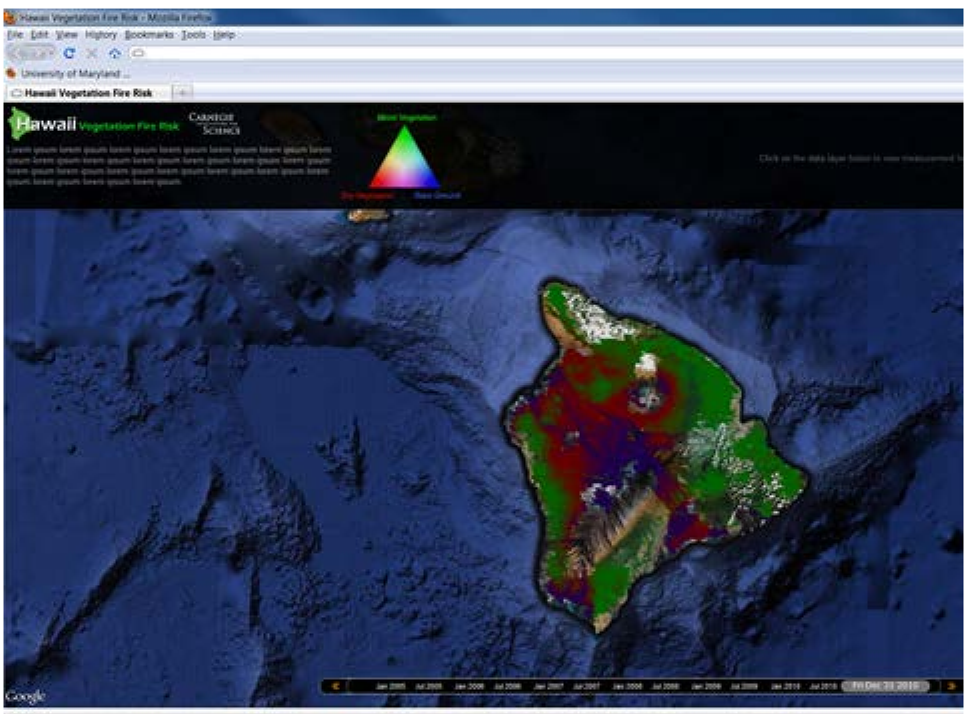

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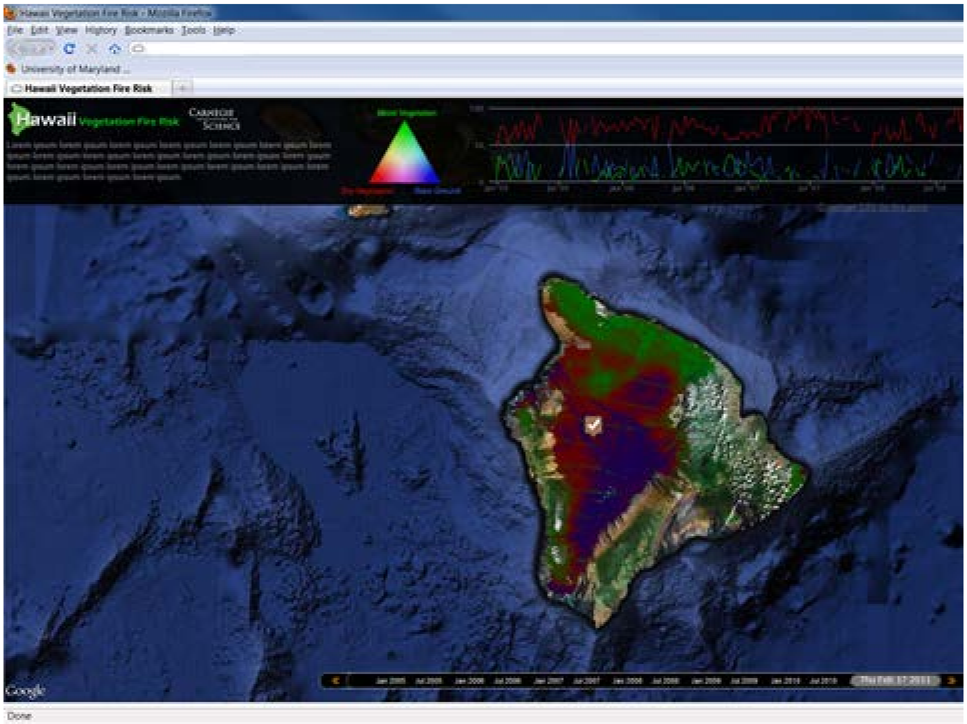
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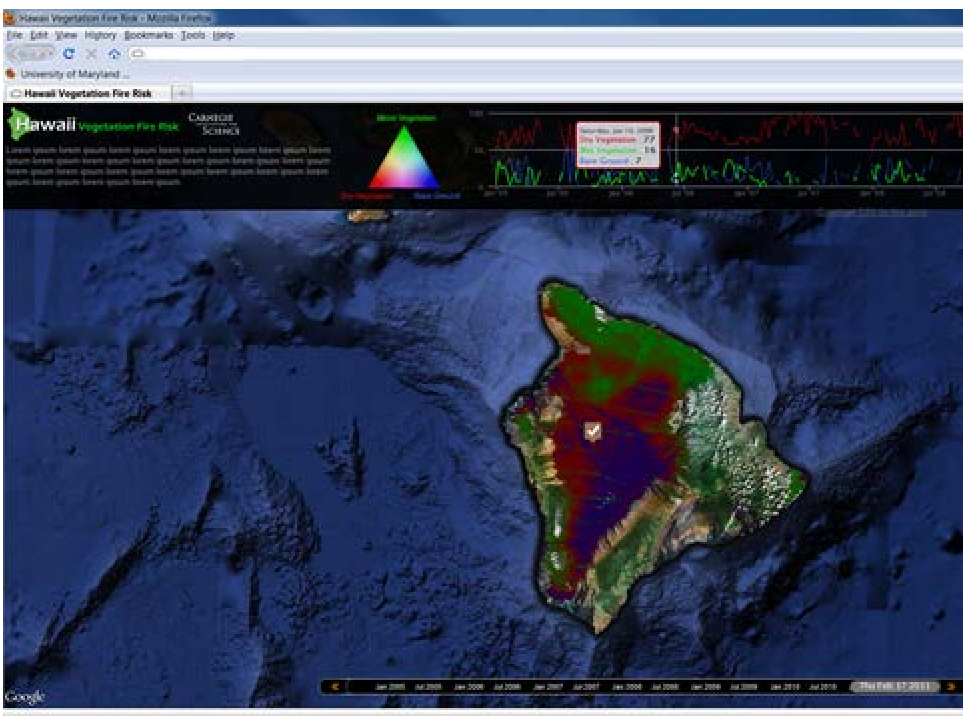
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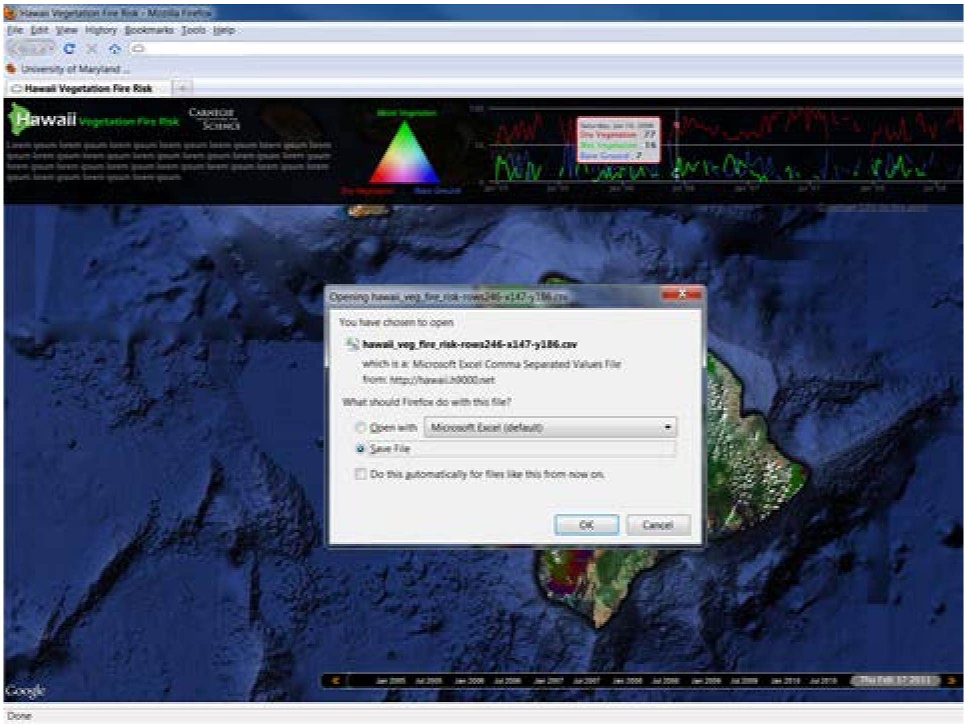
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which is a: Microsoft Excel Comma Separated Values File
from: http://hawaii.h9000.net
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2. Fire Science Workshop

In 2011 we held a workshop on November 18th for all land managers in Hawaii that are concerned with fire. The workshop is titled "New Tools and Approaches to Managing Wildfire Threats in Hawaii, attended by 33 Participants (USFS (7), NPS (1), DoD Contractor (2), DoD (1) DOFAW (8), Watershed Alliance (2), UH (8), Carnegie (1), Other University (1), Non Profit (2) and had the following format:

New science that can improve Fire Forecasting & Modelling Mapping Vegetation and Fire Conditions on the Island of Hawaii:

- Hawaii Wildfire Webtool, Dr. Greg Asner, Carnegie Institution
- Fire Weather, Fire Danger and Fire Behavior Prediction for Hawaii, Dr. Francis Fujioka, USDA Forest Service, PSW Research Station
- Fire modelling using spatial data: Developing maps of canopy fuels parameters, with examples from Lassen Volcanic National Park, Dr. Andrew Pierce, University of Hawaii and USDA Forest Service, PSW-Hilo Research Station

Potential Opportunities and Partnerships:

- Evaluating fire risks using Ecosystem Management Decision Support system, Dr. Paul Hessburg and Dr. Keith Reynolds, USDA Forest Service, PNW Research Station
- The Pacific Fire Science Consortium -the Island's hottest new partnership, Dr. Christian Giardina and Elizabeth Pickett, USDA Forest Service, PSW Research Station and Hawaii Wildfire Management Organization.

Our research based products – supported by this SERDP award – provided the impetus for this workshop and have facilitated a number of exciting and new partnerships. In particular, the development of a recently funded project (funded through the Joint Fire Science Program) - The Pacific Fire Exchange (http://www.pacificfireexchange.org/).The premise and goals of the consortium include: 1) A broad base of Hawaii- and U.S. affiliated island-focused fire science to project impacts of wildfire to the natural resources, human communities, and built environments of the region; 2) A means of transferring knowledge within and among islands and areas of similar fire fuels, fire hazards, and ecoregions; 3) A means of transferring knowledge between scientists, resource managers, decision-makers, fire suppression agencies, and communities in Hawaii and the U.S. affiliated Pacific; and 4) A structured forum and process for identifying and prioritizing critical new areas of fire research. The Hawaii DoD (from PTA, Makua, and Schofield) and scientists from the USDA FS and the University of Hawaii are the project PI's and coordinators.